Competition and Coexistence of Reef-Corals

Thesis submitted by

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Statement of Contribution of Others

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Table I. Statement of contribution to thesis chapters. MAN is Mariana Álvarez Noriega, SRC is Sean R. Connolly, AHB is Andrew H. Baird, MD is Maria Dornelas, and JSM is Joshua S. Madin.

Chapter	**Statement of contribution**
Chapter 1: General introduction	MAN wrote the chapter with feedback from SRC and AHB.
Chapter 2: Fecundity and the demographic strategies of coral morphologies	MAN, SRC, and AHB conceived the research. MAN developed the models under the supervision of SRC. MAN wrote the manuscript with feedback from SRC, AHB, MD, and JSM.
Chapter 3: The effect of competition on coral colony growth and the relationship of competitive ability with demographic rates	MAN and SRC conceived the research. MAN processed the competition data and conducted the statistical analyses under the supervision of SRC. MAN wrote the manuscript with feedback from SRC, AHB, MD, and JSM.
Chapter 4: Disturbance-induced relative nonlinearity of competition promotes coexistence in reef-building corals	MAN and SRC conceived the research. MAN developed the models and the code to quantify the contribution of coexistence-promoting mechanisms under the supervision of SRC. MAN wrote the chapter with feedback from SRC, AHB, MD, and JSM.
Chapter 5: General discussion	MAN wrote the chapter with feedback from SRC.

Thesis abstract

Reef-building coral assemblages can be very species-rich, but the processes maintaining these levels of biodiversity are largely unknown. While understanding the processes that allow species coexistence has been a challenging task for ecologists for many decades, new methods allow the contributions of some coexistence-promoting mechanisms to be quantified. In this thesis, my overarching aim is to investigate how coral biodiversity is maintained: specifically, how environmentally-induced fluctuations in demographic rates influence coral species coexistence. To do this, I: i) quantify the relationship between size and fecundity for eight species of corals (to obtain parameter estimates for competition models) (Chapter 2); ii) test for trade-offs between competitive ability and demographic rates, and test the effect of competition on colony growth (to determine how to characterize competition in my models) (Chapter 3); and iii) evaluate the role of disturbance in promoting coral species coexistence (Chapter 4).

In Chapter 2, I estimated colony fecundity for eight coral species, using a five-year data set of coral demographic rates from Lizard Island, Great Barrier Reef, Australia. I found that size-dependent fecundity is much more similar between species with a similar morphology than among morphologies. This result suggests that colony morphology can be used as a proxy for coral fecundity, as previous work shows that morphology can also serve as a proxy for growth and survival. Using colony morphology as a proxy for coral demographic rates can help coral ecologists simplify the coexistence problem by considering the coexistence of typical species with different growth forms separately from coexistence of species with the same growth form.

In Chapter 3, I investigated the relationship between competitive ability and four important demographic rates: growth, mechanical stability, colony reproductive investment, and number of eggs per colony, by quantifying the proportion of the colony's periphery in competition in photographs of 30 colonies of each of 11 species followed yearly. Results show a trade-off between competitive ability and mechanical stability. However, there was a negligible effect of competition on colony growth, suggesting that any trade-off involving competitive ability in adult colonies is unlikely to influence species coexistence. This result suggests that if competition affects community dynamics, it does so at life-stages other than adults (for instance, via space-limited recruitment, which is well-documented).

In Chapter 4, I used a competition model to investigate the role of hydrodynamic disturbance in coral species coexistence. To describe coral population dynamics, I used integral projection models calibrated with the fecundity estimates obtained in Chapter 2, as well as with growth, survival, and susceptibility to mechanical disturbance estimates already available. I modelled competition via space-limited recruitment (larvae could settle only on space not occupied by resident (juvenile or adult) corals, regardless of the species of the larvae or resident. The model was calibrated for a population with a (mechanically unstable) tabular morphology and a population with a (mechanically stable) digitate morphology. I compared the results of invasibility analyses (to determine whether each competitor has a positive population growth rate when rare) between model scenarios with stochastic mortality induced by hydrodynamic disturbance, and model scenarios with a constant environment. I found that that coexistence was only possible in the presence of environmental fluctuations. There are two fluctuation-dependent mechanisms that could be responsible for this coexistence: the storage effect and relative nonlinearity of competition. The storage effect operates when competition and environmental conditions have subadditive effects on population growth, allowing species to 'store' benefits gained during favourable conditions, and thereby to persist during unfavourable ones. Relative nonlinearity of competition occurs when each competitor performs best at a different resource level, and the resource fluctuates between levels that favour one competitor, and levels that favour its opponent. A partitioning of the contribution of different coexistence-promoting mechanisms indicated that, of the two classes of fluctuation-dependent coexistence mechanisms, relative nonlinearity contributed positively to coexistence, but the storage effect did not.

Explaining biodiversity maintenance in coral assemblages has been a challenging task for coral ecologists. Few coexistence-promoting mechanisms have been tested for reef corals, and most of them have revealed low potential to contribute to coral biodiversity. Consequently, coral species coexistence has remained an enigmatic problem. Disturbance had been hypothesized to play an important role in coral species coexistence for many decades, but its role had been neither mechanistically characterized, nor the magnitude of its contribution quantified. This thesis reveals how coral biodiversity can be maintained by environmental fluctuations. More specifically, it shows that differences in susceptibility to disturbance among corals with different colony morphology can contribute to coexistence via a mechanism called relative nonlinearity of competition. Furthermore, it shows that environmental fluctuations affecting recruitment cannot promote coral species coexistence unless larvae directly compete against each other. Results shed light on how coral

assemblages might respond if disturbance regimes are affected by climate change. Results suggest that predicted changes in the frequency and intensity of hydrodynamic disturbance regimes due to climate change will likely alter competitive dynamics in coral assemblages by increasing the competitive advantage of mechanically robust species.

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Chapter 1: General introduction

1.1 Thesis overview

Reef-building coral assemblages can be very species-rich (hundreds of species; Veron et al. 2011), but the processes maintaining these levels of biodiversity are largely unknown. While understanding the processes that maintain biodiversity has challenged ecologists for many decades, different mechanisms have been proposed and the framework to test their contributions to coexistence has been developed (e.g. Angert et al. 2009, Cáceres 1997; Chesson 1994, Ellner et al. 2016). Consequently, it is possible to at least partly understand the processes contributing to species coexistence in an assemblage (e.g. plants; Levine and Rees 2002, Silvertown 2004, Angert et al. 2009). In this thesis I have employed modern coexistence theory to test the contribution of different processes in maintaining coral biodiversity.

1.2 Coexistence

For coexistence to occur, species must differ in the way they use resources. Such differences can be in performance along a niche axis (niche partitioning; e.g. Silvertown 2004), in the time at which different species use common resources (e.g. Albrecht and Gotelli 2001), in the time at which species are more strongly affected by the biotic and abiotic environment (e.g. Murdoch and Avery 1975, Chesson and Warner 1981), or in species' performance over space (e.g. Tilman 1994). Differences in resource use allow species to coexist when they increase intraspecific competition relative to interspecific competition (i.e. when they have stabilising effects: Chesson 2000a). Additionally, coexistence is facilitated

by reductions in fitness differences among competitors (i.e., equalising effects), essentially by reducing the strength of the stabilising mechanism required for coexistence (Chesson 2000a). Trade-offs are negative interactions between traits, where performing well with respect to one demographic rate (e.g., having higher fecundity, or lower mortality) comes at the cost of performing poorly in another (e.g. Stearns 1989). Trade-offs arise due to physiological or environmental constrains (Tilman 1990), and can lead to both stabilising and equalising effects, playing a key role in species coexistence (Kneitel and Chase 2004).

In nature, different mechanisms can simultaneously affect species coexistence (e.g. Kuang and Chesson 2010, Letten et al. 2018). In modern coexistence theory, coexistence-promoting mechanisms are categorised into mechanisms that do not require environmental fluctuations to operate (i.e. fluctuation-independent mechanisms) and mechanisms that strictly require fluctuations (i.e. fluctuation-dependent mechanisms; Chesson 2000a). Fluctuations can be endogenous (resource fluctuations that are product of community dynamics; Armstrong and McGehee 1980) or exogenous (caused by externally-driven variation in resources or environmental conditions; e.g. Chesson and Warner 1981). Fluctuation-dependent mechanisms are grouped into two classes: the storage effect and relative nonlinearity of competition. The storage effect is a coexistence-promoting mechanism in which population growth is buffered against unfavourable times by storing benefits of favourable years in a life stage that is resistant to fluctuations (Chesson 2000). Relative nonlinearity of competition is a mechanism in which competitors differ in the shape (i.e. nonlinearity) of their response to a limiting factor, allowing each species to perform best at a different level of this limiting factor. Details on how these two mechanisms operate are found in Chapter 4 of this thesis.

Testing coexistence-promoting mechanisms experimentally is only feasible in simple organisms with small body size and short generation times (e.g. protozoa: Gause 1934; yeast:

Letten et al. 2018), for which population-level competition experiments can be conducted in microcosms or mesocosms. For larger, longer-lived or more widely-dispersing organisms, coexistence-promoting mechanisms can be investigated by calibrating competition models with demographic data (e.g. Angert et al. 2009). Competition models allow for manipulation of the (model) system, simulating community dynamics with and without specific coexistence-promoting mechanisms to assess their potential contribution to biodiversity maintenance (e.g. Adler et al. 2010, Ellner et al. 2016). To be useful, competition models must accurately capture the processes affecting community dynamics in nature, which requires sound demographic data and a comprehensive understanding of how competition affects dynamics.

Investigating coexistence and trade-offs among all possible pairs of species is logistically inapplicable for species-rich communities. Recent studies have examined how a small number of easily-measurable species traits influence performance as a function of the abiotic and biotic environment, and then inferring species' demographic rates based on their trait values, obviating the need to estimate directly demographic parameters on a species-by-species basis (i.e. trait-based approaches, e.g. Poorter et al. 2008, Sterck et al. 2011, Adler et al. 2013). For traits to be good predictors of demographic performance, however, they must be strongly linked to the organisms' demographic rates and their interspecific variation must be larger than their intraspecific variation (McGill et al. 2006).

1.3 The role of disturbance in coexistence-promoting mechanisms

Disturbance has long been proposed as a major agent influencing coexistence (e.g., Connell 1978). The 'intermediate disturbance hypothesis' (IDH) proposed that biodiversity peaks at intermediate levels of disturbance because a high frequency of disturbance

eliminates susceptible species, while a low frequency of disturbance allows dominant competitors to exclude inferior ones. The IDH was initially proposed to explain the high biodiversity found in tropical forests and coral reefs. Indeed, in one study, reef-coral biodiversity patterns at the local scale match those predicted by the IDH (Aronson and Precht 1995). However, the IDH has been criticised because a reduction in competition caused by disturbance cannot in itself promote coexistence (Chesson and Huntly 1997, Fox 2013). Nevertheless, disturbance can create the necessary conditions for some coexistence-promoting mechanisms to operate (Fox 2013, Shea et al. 2004). Competition-colonization trade-offs promote coexistence when the superior competitor can displace the inferior competitor, but the inferior competitor is better at colonizing new space. Disturbance clears patches, leaving free space for the inferior competitor to colonize (Tilman 1994). Additionally, disturbance is a source of environmental variability that can contribute to coexistence via two distinct mechanisms: the storage effect and relative nonlinearity of competition. These two fluctuation-mediated mechanisms are explained and explored in more detail in Chapter 4.

1.4 Competition and coexistence in reef-building corals

In sessile communities, competition can be particularly important in shaping community structure (e.g. Connell 1961). For coral assemblages, suitable space on the substratum is a limiting resource that strongly determines the light and flow conditions to which colonies are exposed. Light and flow influence a colony's ability to capture resources and withstand disturbances, resulting in strong effects on demographic rates (Madin et al. 2012a, Schutter et al. 2010). Despite corals competing for a few limiting resources,

biodiversity can be very high. Therefore, most species should at least partly overlap in resource requirements.

Some coexistence-promoting mechanisms have been tested in coral assemblages. Neutral theory proposes that fitness differences among individuals are negligible and species have perfectly overlapping niches (Hubbell 2001). According to Neutral theory, species richness is maintained by random ecological drift where extinction events are balanced by speciation events. Consequently, it cannot explain coexistence of a specific set of species, since extinction and speciation create a turnover in species composition; thus, it is a qualitatively different explanation than those offered by most ecological coexistence theory. However, the contribution of neutral dynamics to coral biodiversity has been challenged, since patterns of community similarity and species' relative abundances in coral assemblages differ markedly from predictions from neutral dynamics (Dornelas et al. 2006, Connolly et al. 2017). Indeed, neutral theory appears unable to explain the high level of heterogeneity of species abundances in marine systems in general (Connolly et al. 2014).

Intransitive competition (where species A wins over species B, species B wins over species C, but species C wins over species A) can also promote biodiversity maintenance (Gilpin 1975, Laird and Schamp 2006) and has been proposed to operate on coral reefs. Intransitive loops can promote coexistence because each species' population is regulated by at least one other competitor. Although there is evidence for competitive intransitivity in cryptic coral reef invertebrates (Buss and Jackson 1979), reef-building coral show much less evidence of this (Connell 1976). Moreover, the requirements for intransitivity to promote coral species coexistence are very restrictive, and factors that can explain non-transitivity in coral competition, as size-dependent competitive outcomes, are not coexistence-promoting (Connolly and Muko 2003).

The Janzen-Connell hypothesis is another diversity promoting mechanism that has been tested in a coral assemblage (Marhaver et al. 2013). The Janzen-Connell hypothesis proposes that seeds and seedlings suffer higher mortality if found nearby a conspecific adult, than if found near a hetero-specific adult, because the conspecific adult attracts species-specific predators or pathogens (Janzen 1970, Connell 1971). As a species become abundant, suitable space for its seedlings to survive decreases, giving rare species an advantage and allowing them to recover from low densities. In corals, *Orbicella faveolata* planulae and settlers had a lower survival near a conspecific adult compared to near a heterospecific adult (Marhaver et al. 2013). The authors of the study claimed that this was evidence that the Janzen-Connell hypothesis could operate in coral assemblages.

Finally, both recruitment and mortality exhibit substantial fluctuations in coral assemblages, fluctuation-dependent mechanisms might therefore be an important contributor to coral coexistence. However, the contribution of fluctuation-dependent mechanisms has yet to be tested explicitly in reef coral assemblages. Strictly experimental approaches to investigate the contribution of fluctuation-dependent mechanisms to coral coexistence are unfeasible due to the temporal and spatial scales of coral community dynamics. That is, it is logistically unfeasible to run long-term, whole population-level competition experiments under controlled experiments, as in, e.g., Tilman's classic experiments on resource competition in phytoplankton (e.g., Tilman 1982). Consequently, a competition model must be calibrated to test hypothesis about the role that disturbance plays in coral species coexistence (*sensu* Angert et al. 2009, Miller et al. 2011). For reef-building corals, long-term estimates of growth and survival parameters are available for a series of species on the reef crest of Trimodal Reef (Lizard Island, Great Barrier Reef) (Dornelas et al. 2017, Madin et al. 2014), a species-rich assemblage (Dornelas and Connolly 2008). However, size-dependent fecundity estimates are also required.

The competition model must capture competitive dynamics in natural communities. Larval recruitment decreases with increasing proportion of space occupied (Connell et al. 1997), indicating that density-dependent settlement must be included in the model. Adults compete by growing above competitors and shading them (without direct contact), or directly by overgrowing neighbouring colonies or digesting their tissue. Competition for space among adult corals can cause a negative effect on colony growth (Elahi 2008, Romano 1990, Tanner 1997). Such demographic effects of competition suggest that dominant competitors can displace (overgrow or overtop) subordinate ones, a requirement for competition-colonization trade-offs to contribute to species coexistence. However, most of the evidence for such displacement comes from experimental studies that used high levels of competition, which are not necessarily representative of most levels of competition experienced in the field.

Wave action is one source of disturbance on coral reefs, particularly important on the reef-crest. Mechanical disturbance produced by waves affects corals differently depending on their morphology and colony size (Madin and Connolly 2006), and it is an significant source of coral mortality (Madin et al. 2014). Top-heavy colonies are more likely to be dislodged than bottom-heavy ones, and therefore large arborescent and tabular colonies are particularly susceptible to dislodgments during major storms and cyclones. Tabular and branching corals can dominate undisturbed reefs, but suffer the highest mortalities after hydrodynamic disturbances (Porter et al. 1981). The size-dependent periodic removal of dominant competitors has the potential to create the necessary conditions for fluctuation-dependent coexistence-promoting mechanisms to operate.

1.5 Thesis outline

The overarching aim of this thesis is to investigate the processes maintaining the high biodiversity found in coral communities. To do this, I have addressed four specific aims in four data and modelling chapters, as follows:

In **Chapter 2**, I test how well morphology predicts the colony size-fecundity relationship in eight species of broadcast-spawning corals. Variation in colony fecundity is substantially greater among species with different morphologies than between species with a similar morphology, demonstrating that colony morphology can be used as a quantitative proxy for size-dependent fecundity. Additionally, I examine the relationship between size-specific colony fecundity and mechanical vulnerability (i.e., vulnerability to colony dislodgment). Interestingly, the relationship between size-specific fecundity and mechanical vulnerability varied qualitatively among morphologies. For tabular species, the most fecund colonies are the most mechanically vulnerable, while the opposite is true for massive species. For corymbose and digitate colonies, mechanical vulnerability remains relatively constant as fecundity increases. These results reveal strong differences in the demographic trade-offs among species of different morphologies. Using colony morphology as a quantitative proxy for demographic strategies can help predict coral community dynamics and responses to anthropogenic change.

In **Chapter 3**, I use a 5-year data set that includes 11 coral species on the reef crest at Lizard Island on the Great Barrier Reef to test whether species differ in competitive ability either in direct-contact (overgrowth and digestion) or overtopping competition. The results show that species of the same morphology have similar competitive abilities. Tabular and branching colonies were the best overtoppers, while massive colonies won most of the direct-contact encounters. However, since overtopping was vastly more common than direct-contact

encounters, the better overtoppers had a competitive advantage. Additionally, I test whether colonies were more likely to compete with other colonies of a similar morphology than with colonies from other morphological groups. If competitive dominants aggregate and are disproportionally more likely to compete against each other than against other morphologies, the effect of superior competitors on inferior competitors is reduced. Tabular colonies were disproportionally more likely to compete against one another than with other morphologies, increasing intra-morphological relative to inter-morphological competition of the dominant competitors. Moreover, I investigate the relationships between competitive ability and three key traits: growth rate, mechanical stability and fecundity. Good competitors grew more quickly and had higher fecundity but were less mechanically stable, implying a trade-off between performance during disturbance vs. performance in the absence of disturbance. Finally, I quantified the effect of competition on growth. Results show a negligible effect of competition on growth, implying that trade-offs involving competitive abilities in adult colonies are unlikely to influence community dynamics and that if competition does affect demography, it is more likely to do so at life-stages other than adults.

In **Chapter 4**, I use the growth and mortality estimates already available (Dornelas et al. 2017, Madin et al. 2014), along with the fecundity estimates obtained in Chapter 2 to calibrate a competition model and analyse coexistence between coral species. Since the results of Chapter 2 suggest that colony morphology is a good proxy for demographic rates, I simulate competition between two model species with different morphologies, one that is susceptible to mechanical disturbance (tabular) and one that is resistant to it (digitate). In the simulations, I included dislodgement of colonies due to wave action, whose strength fluctuated every year. I tested whether the two competing species could coexist in the presence and in the absence of these yearly fluctuations. I found that coexistence was only possible in the presence of environmental fluctuations, indicating that fluctuation-dependent

mechanisms were responsible for coexistence. Consequently, I quantified the contribution of each fluctuation-dependent mechanism (relative nonlinearity and the storage effect) to coexistence. The results indicated that relative nonlinearity prevented the extinction of the digitate species. The results from this chapter imply that, as frequency of intense storms increases with climate change, the competitive advantage of the tabular species might not be sufficient to secure its persistence.

1.6 Publication details

Chapters 2 and 3 have been published in the journal Ecology (Álvarez-Noriega et al. 2016 and Álvarez-Noriega et al. 2018, respectively). They have been written and formatted to fit the journal's guidelines.

Chapter 2: Fecundity and the demographic strategies of coral morphologies

2.1 Introduction

Understanding how differences in demographic strategies of organisms are related to functional traits can illuminate the processes shaping community structure. Recent studies have shifted the focus towards the interaction of these traits with the abiotic and biotic environment, and away from species-by-species examination of demographic responses to the environment (McGill et al. 2006, Adler et al. 2013). A functional trait is a readily measurable characteristic of an organism that affects its fitness (McGill et al. 2006). For example, phytoplankton species with large cell sizes have a slower maximum growth rate than species with small cell sizes (Edwards et al. 2012). For a trait-based approach to be informative of community processes, there must be a strong relationship between the trait and demographic strategies. Consequently, the first step in trait-based approaches is to test whether demographic strategies are more similar between species that share the same functional trait than between species that diverge in functional traits. Trait-based approaches have been used to identify mechanisms maintaining biodiversity (Angert et al. 2009) and in explaining community composition across gradients (Moles et al. 2011, Edwards et al. 2013).

Demographic strategies are the possible pathways in the relationship between demographic rates and age or size that an organism can take (Pianka 1971). Trade-offs arise when good performance of one ecological function by one trait compromises the performance of another ecological function by another trait (Stearns 1992). Traits have complex interactions and covariations with one another and negative interactions among

some traits can result in positive interactions among others (Reznick et al. 2000). Examples of demographic trade-offs are growth rate vs. tolerance to low resource levels (Teuschl et al. 2007), food acquisition vs. predation risk (Laurila et al. 2008), and number vs. size of offspring (Marshall and Keough 2005). Trade-offs can favour species coexistence by reducing differences in fitness between competing species, and by giving different species advantages under different environmental conditions (equalizing and stabilizing effects, respectively, *sensu* Chesson 2000a). Trade-offs can also influence which species are winners and losers as a consequence of environmental change, and thus influence community structure (Tilman and Pacala 1993).

Most trait-based approaches investigating demographic trade-offs have been conducted on plants. For example, wood density is positively related to mechanical support and resistance to rupture (Hacke et al. 2001) and negatively related to growth rate (Poorter et al. 2008), resulting in a trade-off between survival and growth (Wright et al. 2010, Philipson et al. 2014). Some studies have gone a step further and linked demographic trade-offs to community ecology. Traits have been linked to environmental variables to explain the distribution of plant species (Pavoine et al. 2011, Sterck et al. 2011). Similarly, trait-based approaches have been used to identify the processes that contribute to community assembly in woody plants (Ackerly and Cornwell 2007, Kraft et al. 2008). Trait based approaches are likely to be particularly fruitful in species rich assemblages, such as reef corals, because it is impractical to quantify demographic rates on a species-by-species basis. Additionally, trait-based approaches reduce the negative impacts of destructive sampling and build the foundation for a predictive framework for community dynamics (McGill et al. 2006).

In reef corals, many demographic rates are qualitatively associated with colony morphology (Jackson 1979, Hughes and Jackson 1985). Coral species can be grouped into a number of different morphologies, which often have similar demographic rates and responses

to disturbance. Morphology is a good predictor of colony growth rate (Darling et al. 2012, Pratchett et al. 2015, Madin et al. 2016) and mortality (Madin et al. 2014). Additionally, competitive dynamics are influenced by the morphology of competitors (Lang 1973, Porter 1974). Therefore, colony morphology is a promising trait to use as a quantitative for demographic strategies in corals.

Corals are colonial organisms composed of polyps. Polyp maturity is determined by colony size (Kojis and Quinn 1984, Sakai 1998) and polyp age (Kai and Sakai 2008, Graham and van Woesik 2013). The number of gametes per polyp is strongly limited by polyp volume and gamete size, and these constraints vary among species and genera (Harriott 1983, Hall and Hughes 1996). In general, energy content per gamete trades off against the number of gametes produced, and gametes with higher energy content are thought to have higher survival (Stearns 1992). Although there is no evidence for a fitness advantage with increasing gamete size in broadcast-spawning corals (Graham et al. 2008, Graham et al. 2013), higher survival in better-provisioned offspring has been observed in other marine invertebrates (Jarrett and Pechenik 1997, Jarrett 2003, Marshall et al. 2006) and plants (Saverimuttu and Westoby 1996, Moles et al. 2004).

Population dynamics depend on two fundamental demographic processes: births and deaths. Trade-offs between fecundity and mortality are common in many organisms (Schluter et al. 1991). On reefs, one major cause of mortality is hydrodynamic disturbance (De'ath et al. 2012). If strong, wave action can dislodge or break off coral colonies. The effects of hydrodynamic forces on coral colonies depend on the strength of the colony's attachment to the substrate (Massel and Done 1993) and on the colony's morphology (Madin and Connolly 2006). Wave action is an important factor shaping the size-structure and zonation patterns of species across the reef (Madin and Connolly 2006, Done 1982). Size-dependent mortality

rates are closely linked to the effects of wave action on colony morphology (Madin et al. 2014).

Here, I assess whether colony morphology influences the relationship between colony size and colony fecundity, and I characterize quantitatively the demographic trade-off between colony fecundity and colony vulnerability to dislodgment during hydrodynamic disturbance. I used a five-year data set, comprising four different morphologies with two coral species each. My findings support to the hypothesis that morphology is good proxy for demographic traits: they show that fecundity schedules are strongly associated with colony morphology, and, more broadly, they move beyond our existing qualitative understanding to quantitatively characterize how morphology influences demographic trade-offs in reef-building corals.

2.2 Methods

2.2.1 Study location and data collection

The data were collected on Lizard Island in the northern Great Barrier Reef, from 2009 to 2014. The study site was located along 200m of the northern semi-exposed reef crest between Palfrey Island and South Island (14.699839°S, 145.448674°E).

Corals are colonial organisms formed by the aggregation of polyps. In general, most polyps within a colony produce oocytes and therefore colony fecundity increases as colony size increases. Exceptions include the sterile zone on the tips of the branches within *Acropora* colonies (Wallace 1985) and the perimeter of massive colonies (Sakai 1998). However, comparisons among species are complicated by the fact that both polyp (Veron 2000) and oocyte size (Harrison and Wallace 1990) vary greatly among species. Even though there is no evidence linking oocyte size to larval survival in broadcast-spawning corals (Graham et al.

2008), it is possible that oocyte size affects early post-settlement survival. If oocyte size has no effect on fitness, the number of oocytes per colony would be a demographically meaningful currency for colony fecundity. In contrast, if oocyte size and provisioning strongly influences early post-settlement survival, oocyte energy content may be more demographically meaningful than the number of oocytes per colony. For that reason, I used both currencies to measure colony fecundity: number of oocytes per colony and colony reproductive investment. I define colony reproductive investment as the number of oocytes per polyp, multiplied by the number of polyps in the colony and by the average carbon content per oocyte. All analyses were done twice, once with each currency.

Thirty colonies from 8 common species grouped into four morphologies were sampled each year from 2009 to 2014: tabular (*Acropora cytherea* and *A. hyacinthus*), corymbose (*A. nasuta* and *A. spathulata*), digitate (*A. humilis* and *A. cf. digitifera*) and massive (*Goniastrea pectinata* and *G. retiformis*; Fig. 2.1). All species are broadcast spawning hermaphrodites and the sampling occurred in the week before spawning occurred in all years. For the *Acropora* spp., four branches were removed from near the centre of the colony, fixed and decalcified. Then, the number of oocytes in each of 6 polyps per branch, selected at random from below the sterile zone (Wallace 1985), were counted under a dissecting microscope. For the *Goniastrea* spp., one nubbin containing approximately 20 polyps was removed from each colony and the number of oocytes in six randomly selected polyps was determined as above. The sampled colonies were photographed with a scale bar and the photographs were corrected for barrel distortion. From the photographs, the contours of the focal colonies were outlined and the areas were compared to that of the scale to estimate the colonies' planar area using ImageJ.

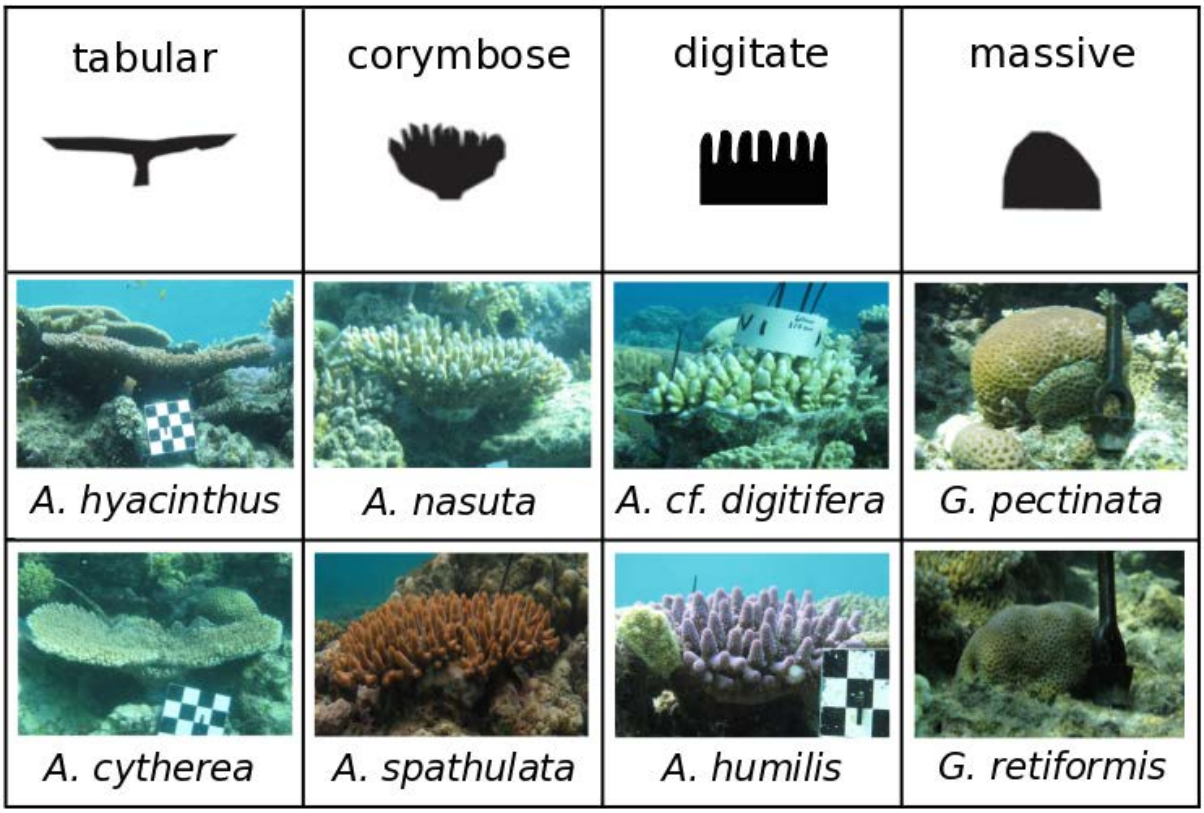

Figure 2.1 Stylized illustrations of the different colony morphologies in this study. The species representing each morphology are listed below each illustration with the respective side-on photo of the species at the site.

To estimate the number of polyps per colony, I estimated the average polyp density for each species and multiplied this by the colony size. Polyp densities were estimated by counting all the calices inside a projected area of 16cm^2 in replicate coral skeletons for each species from colonies collected at the study site.

To estimate the proportion of polyps outside the sterile zone, the length of the sterile zone and colony depth had to be estimated. The length of the sterile zone in *Acropora* spp. was measured as the distance from the tip of the branch to the first polyp with oocytes. Colony depth was measured from the coral skeletons. Massive colonies generally have immature polyps in the borders of the colony (Sakai 1998), but the size of the sterile zone could not be determined because nubbins were generally collected from the centre of the

colony. Here, I assumed the sterile zone for the massive species to be zero, but this bias is reduced as colony size increases and the ratio of perimeter to area decreases.

To estimate oocyte carbon content, four to six colonies from each species were collected and placed in an outdoor flow-through aquarium a few days before spawning in 2013 and 2014. Prior to spawning, the colonies were isolated in individual buckets. Gamete bundles from each colony were collected and washed in 0.2 µm filtered seawater (FSW) to break apart the bundles and clean away the sperm. Five eggs from each colony were transferred individually into pre-cleaned tin capsule (ATD-1027 Tin Capsule Pre-Cleaned 6 x 4 mm; Choice Analytical) and frozen in liquid N_2. Since blank readings on each plate vary, five blank controls (capsule with no egg) for each plate were also sampled. Total carbon content of each egg was analyzed on a solid sample combustion unit (Shimadzu) at the Australian Institute of Marine Science.

2.2.2 Statistical analysis

The distribution of the number of oocytes per polyp was bimodal for all species, with one of the modes being zero. I used a zero-inflated linear model, in a Bayesian framework, to account for this large number of zero counts. The zero-inflated model includes two steps: the first step analyses the zero vs. non-zero data which gives a posterior distribution of the parameter estimates predicting the probability of a polyp being fecund, and the second step analyses variation in counts for the non-zero observations which gives the posterior distribution of the parameter estimates predicting the number of oocytes per fecund polyp. The models were first fitted for each species separately, and then for each morphology, grouping the pairs of species of each morphology. Both components of the zero-inflated model were explicit functions of colony size (as m^2 on a natural logarithmic scale) and the relationship was constrained to be zero or positive. The analysis was performed in R version

3.1.2 (R Core Team 2013), with the function ‘logit’ from the package ‘BayesLogit’ (Polson et al. 2013) being used for the binomial regression. The number of oocytes was estimated by maximising the zero-truncated poisson log-likelihood. For the massive species, a zero-truncated negative binomial log-likelihood was used instead because the data were overdispersed. The Markov Chain Monte Carlo chains were generated with a Metropolis algorithm with the function ‘MCMCmetrop1’ from the package ‘MCMCpack’ (Martin et al. 2011). Similarly, I estimated the colony depth, the length of the sterile zone, polyp density, and carbon content per oocyte assuming a Gaussian distribution. All priors were uninformative. All parameter estimates are found in the Tables A.1-A.5 in Appendix A-Chapter 2.

To estimate fecundity at the colony level, I had to combine information from multiple analyses: probability of fecundity as a function of colony size, number of oocytes per mature polyp as a function of colony size, polyp density, length of sterile zone, colony depth and energy content of eggs. Each of these quantities has uncertainty associated with it, and each of these uncertainties propagates through to the overall fecundity-colony size relationship. To rigorously account for this propagation of uncertainty, I employed a Bayesian approach. Bayesian methods yield a posterior probability distribution of parameter values, given the data and any prior beliefs about those parameters. (I used uniform priors, to ensure that the posterior distribution depended only on the information in the data analyzed in this study.) To account for the propagation of uncertainty, I randomly selected, from my analyses of each component of colony fecundity, a set of parameters from the model fit’s posterior distribution, and I used these to compute colony fecundity as a function of size. By repeatedly and randomly selecting parameter sets from the relevant posterior distributions, I obtained a distribution of estimates of the colony size-fecundity relationship, from which I calculated the median and the 95% credible interval (0.975 and 0.025 quantiles).

To estimate the number of oocytes per colony, I multiplied the probability of a polyp being fecund, the number of oocytes per fecund polyp, and the number of fecund polyps in the colony. To estimate reproductive investment at the colony level, I multiplied the number of oocytes per colony and the average carbon content per oocyte. To estimate the number of fecund polyps in the colony, I multiplied the polyp density (polyps/cm^2), the proportion of the polyps outside the sterile zone (1- length of the sterile zone/colony depth), and the size of the colony (in cm^2).

I calculated differences in colony size-fecundity relationships (with fecundity measured both as number of oocytes per colony and as reproductive investment) in the following fashion. To estimate the differences in colony fecundity between species, I drew randomly from the posterior distribution of the size-fecundity relationship for each species, and I calculated the difference between the colony fecundity of the two species as a function of size. By repeating this process 1000 times, I obtained a posterior distribution of differences in colony fecundity. Differences in colony fecundity between morphologies were estimated in analogous fashion. If the 95% credible interval did not overlap zero, I inferred that the colony size-colony fecundity relationships were different.

To investigate the demographic strategy of species with respect to mechanical vulnerability and colony fecundity, I examined the relationship between colony shape factor (CSF) and colony fecundity across all observed sizes. CSF is a dimensionless measurement of mechanical susceptibility that has been developed for different coral morphologies (Madin and Connolly 2006). Larger CSF values correspond to higher mechanical vulnerability. CSF is reduced by wide colony bases and increased by increasing colony height and increasing colony width above the base relative to the width of the base. For example, tabular colonies, which are top-heavy, are more susceptible to mechanical disturbance and have a higher CSF than massive colonies, which are bottom-heavy. The different morphologies have different

colony size-CSF relationships. As tabular and corymbose colonies grow, the weight of the top of the colony increases with respect to the base and therefore they become more vulnerable to mechanical dislodgment. In contrast, the base of digitate and massive colonies becomes wider with increasing colony size, and the CSF decreases. I used previously estimated CSF values for the same species at this site (Madin et al. 2014).

2.3 Results

Despite strong differences among species in the probability of a polyp being mature (Fig. 2.2-a) and differences in the number of oocytes per mature polyp (Fig. 2.2-b; Fig. A.2), the relationships between colony reproductive investment and colony size converged strongly in slope and intercept among most species (Fig. 2.2-c). However, there was somewhat more variation among species in the relationship between the number of oocytes per colony and colony size (Fig. 2.2-d). Massive species had a two order-of-magnitude advantage in the number of oocytes per fecund polyp over the rest (Fig. 2.2-b) but they had low polyp density (due to large polyps; Table A.3), and the lowest carbon content per egg (Table A.4). The opposite was true for the tabular species. Species within morphology were not evidently more similar to each other than to species of different morphology in polyp maturity and number of oocytes per mature polyp, except for the digitate species, which had very similar polyp maturity probabilities (Fig. A.1).

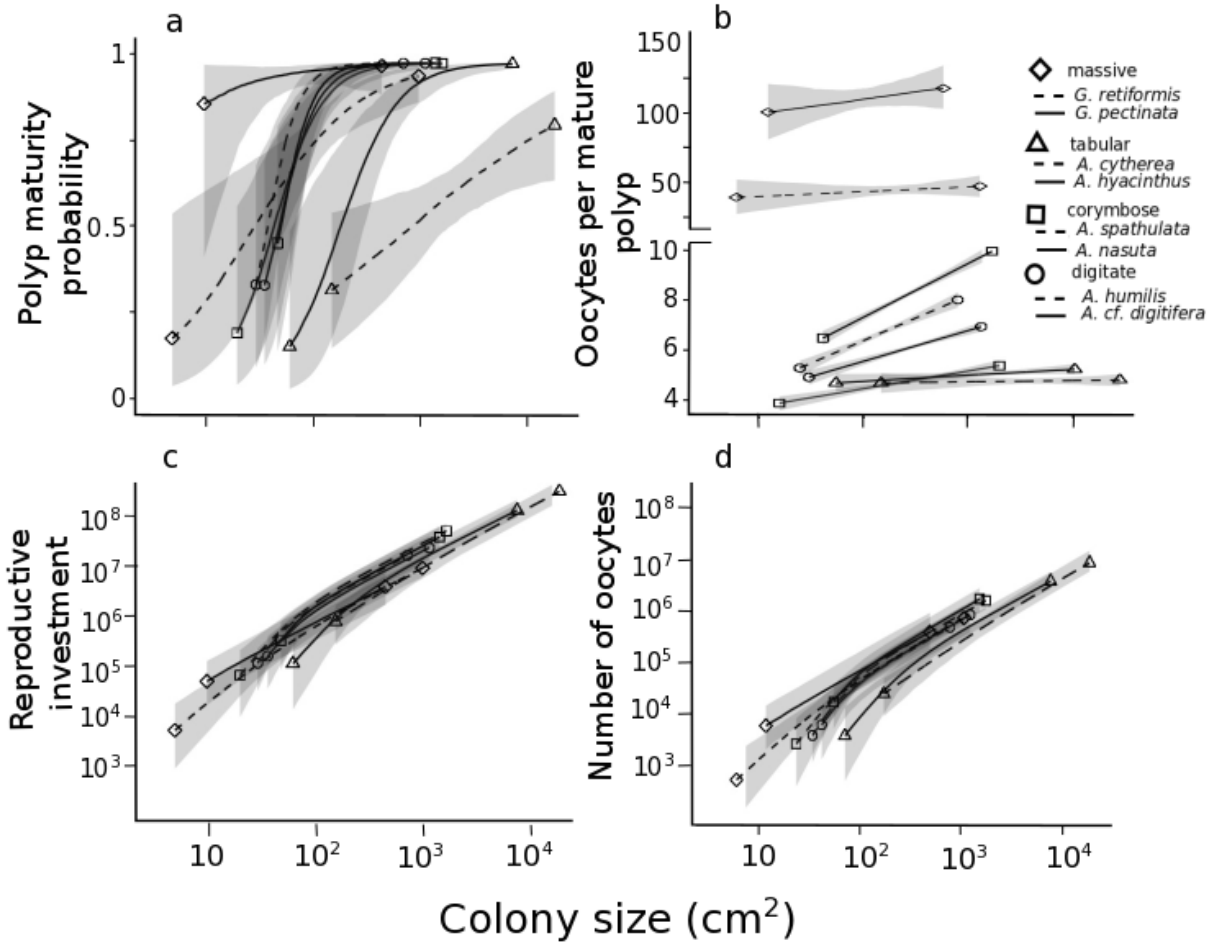

Figure 2.2 Fecundity as a function of colony size. (a) probability of a polyp being mature vs. colony size (log scale). (b) number of oocytes per mature polyp vs. colony size (log scale). (c) reproductive investment (μg carbon) vs. colony size (log-log scale). (d) number of oocytes per colony vs. colony size (log-log scale).

Overall colony reproductive investment and the number of oocytes per colony were more similar between species of the same morphology than among morphologies (Fig. 2.3). The 95% credible interval of the differences in colony reproductive investment and the number of oocytes per colony between species of the same morphology overlapped zero in all cases (Fig. 2.3). When comparing among morphologies, massive colonies had the lowest reproductive investment, followed by tabular colonies, while corymbose and digitate colonies had the highest reproductive investment (Fig. 2.3). In contrast, massive colonies had the highest number of oocytes per colony, while tabular colonies had the lowest number of oocytes per colony (Fig. 2.3).

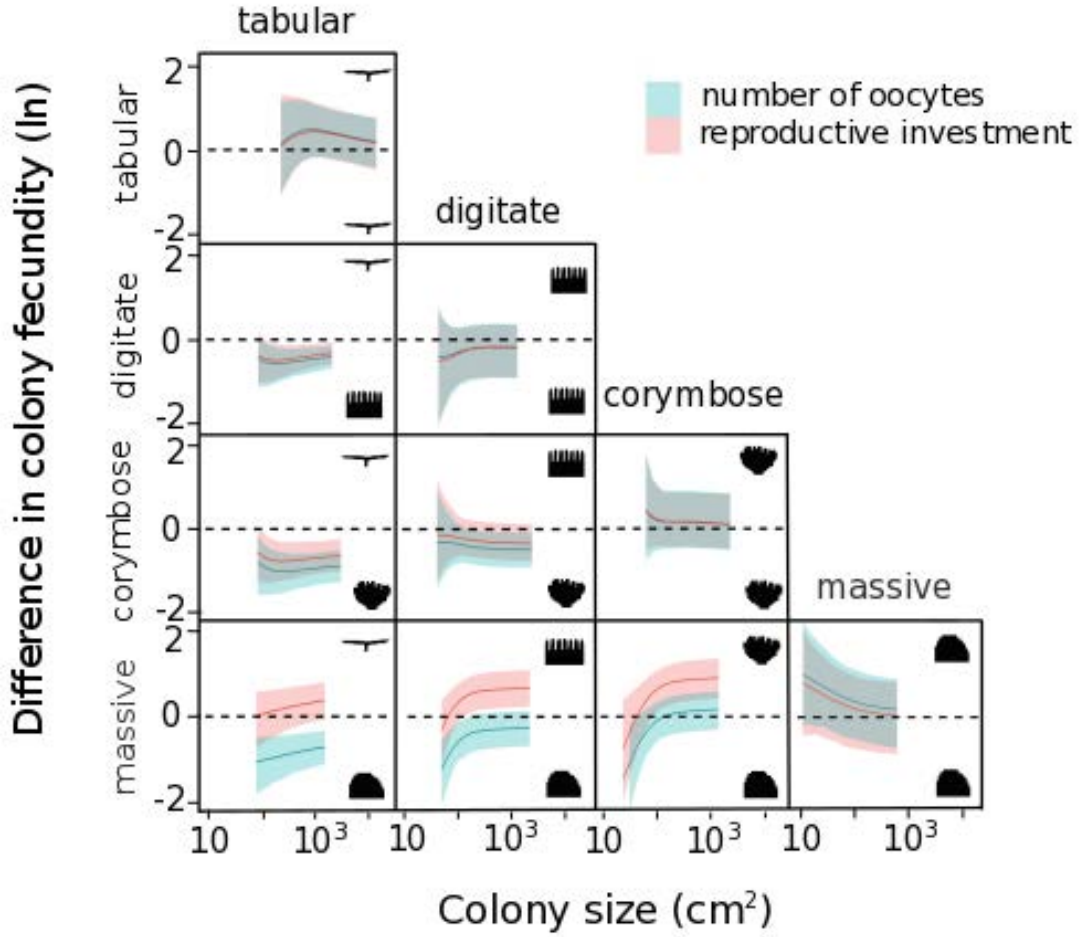

Figure 2.3 Differences in fecundity vs. colony size (log-log scale). Light red corresponds to the analysis where fecundity is in terms of reproductive investment (μg carbon). Blue corresponds to the analysis where fecundity is in terms of the number of oocytes produced per colony. The panels in the upper right diagonal correspond to comparisons between species within morphology. The top left panel corresponds to the colony fecundity of *A. hyacinthus* minus *A. cytherea*. The second panel in the diagonal corresponds to the colony fecundity of *A. cf. digitifera* minus *A. humilis*. The third panel in the diagonal corresponds to the colony fecundity of *A. spathulata* minus *A. nasuta*. The bottom right panel and final panel in the diagonal corresponds to the colony fecundity of *G. pectinata* minus *G. retiformis*. The panels below the diagonal correspond to the between-morphology differences in fecundity vs. colony size. Thus, for example in the bottom left panel, tabular colonies have higher reproductive investment than massive colonies but fewer oocytes. The colony fecundity from the morphology illustrated on the bottom of each panel is subtracted from the colony fecundity of the morphology illustrated on the top of each panel. The shaded areas show the 95% credible interval. The dashed lines mark zero difference in colony fecundity.

Within each morphology, species had very similar relationships between CSF and colony reproductive investment (Fig. 2.4-a) and between CSF and the number of oocytes per colony (Fig. 2.4-b). However, the different morphologies occupied very different areas of

demographic trait space. In the massive species, colony reproductive investment and number of oocytes per colony increased as colonies became more stable (i.e. as CSF decreased). Digitate and corymbose species maintained a relatively constant mechanical stability, regardless of colony reproductive investment and number of oocytes per colony. In the tabular species there was a trade-off between stability and fecundity: as colonies became more fecund, they also became less stable.

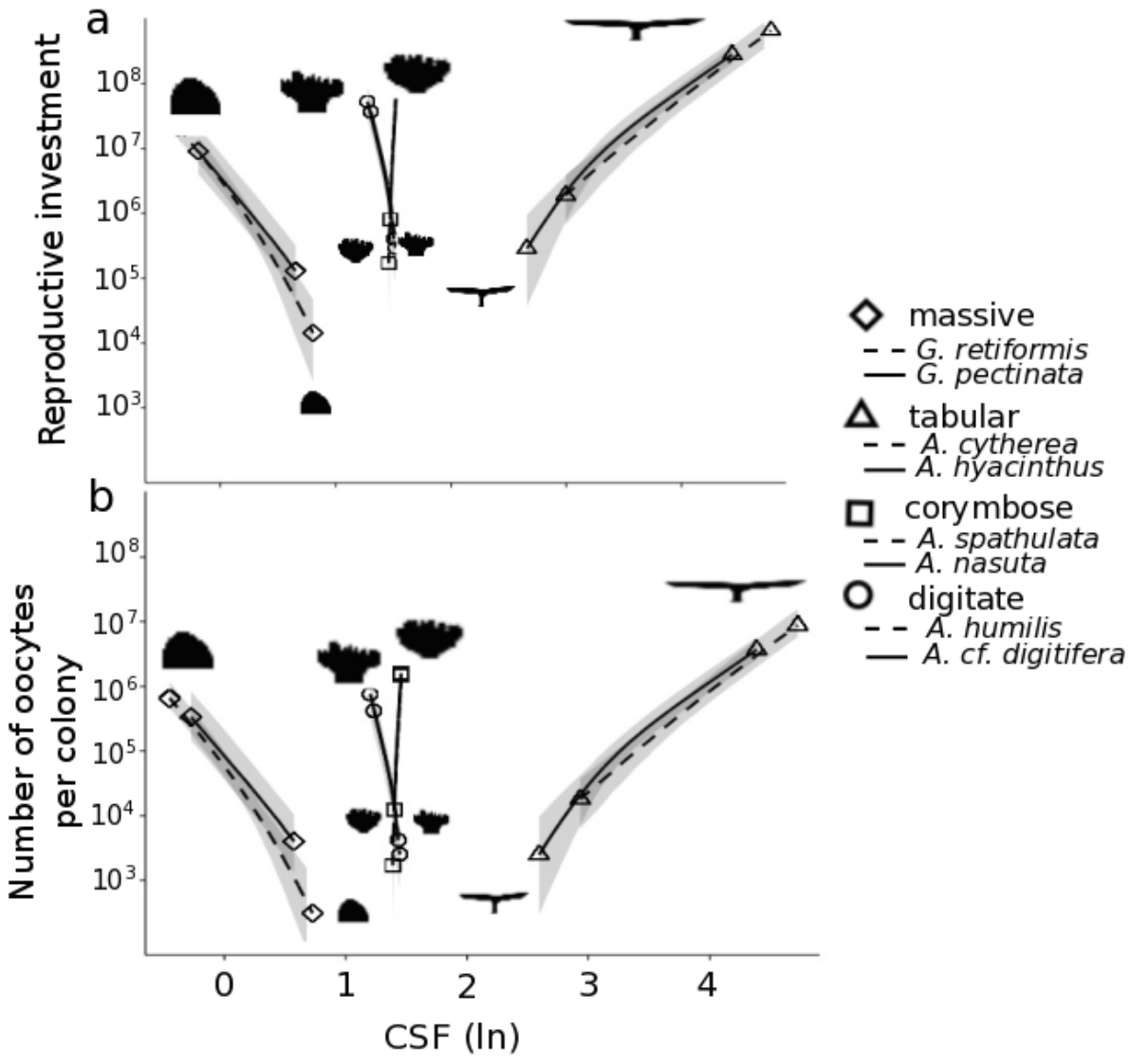

Figure 2.4 Relationship between fecundity and mechanical stability. (a) reproductive investment (μg carbon) vs. CSF (log-log scale). (b) number of oocytes per colony vs. CSF (log-log scale). The size of the growth forms shows the direction of the increase in colony size. The grey area shows the 95% credible interval. Colonies with high CSF values are more easily dislodged than colonies with low CSF values.

2.4 Discussion

The relationship between colony size and reproductive investment was very similar among species. This finding was remarkable, given the strong differences in the individual component relationships (colony size vs. maturity probability; colony size vs. number of oocytes per mature polyp). The similarity in size- reproductive investment relationship between species may be caused by trade-offs between the number of oocytes per polyp, the number of polyps per unit of projected area and the carbon content per oocyte. Massive colonies produced the highest number of oocytes per polyp, but invested the least amount of carbon per oocyte and had the lowest polyp density. In contrast, tabular colonies had the lowest number of oocytes per polyp but invested the most energy into each oocyte. While morphologies that invest in the number of oocytes will benefit by having a higher abundance of potential offspring, morphologies that invest in the quality of the oocyte may benefit from increased survival of the oocyte due to increased energy reserves and consequently a higher probability of fertilization, larval survival or early post-settlement survival. Larger larval size has been linked to increased growth in barnacles (Jarrett and Pechenik 1997, Jarrett 2003), and larger egg size results in higher survival in plants and bryozoans (Moles et al. 2004, Marshall et al. 2003, respectively). However, for broadcast-spawning corals, there is some evidence that no such relationship holds for larval survival (Graham et al. 2008), but potential effects on between-species variation in post-settlement survival have not been studied.

Different coral growth forms follow different demographic strategies, whereas species with the same growth form follow strikingly similar strategies. The trade-offs found between growth forms involving mechanical vulnerability have long been considered coexistence-promoting. For example, a trade-off between mechanical vulnerability and competitive ability allows staghorn colonies dominate in undisturbed environments, but be

disproportionately dislodged by storms (Connell 1978, Connell et al. 2004). My results support the use of colony morphology as a partial proxy for demographic strategies, because colony reproductive investment, the number of oocytes per colony, and the colony fecundity relationships with CSF are consistent between species of the same morphology but differ between morphologies. This finding closely parallels a recent analysis of mortality (Madin et al. 2014), and highlights the potential role of colony morphology in future trait-based approaches in coral reef ecology. The massive species in this study belonged to the same genus to be consistent with my approach for the other growth forms. Because corals with a massive morphologies are present in many branches of the coral phylogeny, it is likely that a broader diversity of colony size-fecundity relationships, and fecundity-mechanical vulnerability trade-offs, exist among massive corals in general, compared to those found here for the genus *Goniastrea*.

Colony morphology has some limitations as a proxy for demographic rates. For continuous traits, such as body size, relationships with demographic rates can be established by fitting a single functional relationship (McGill et al. 2006). In contrast, there is no commonly accepted continuous index or measurement of morphology and each demographic rate must be estimated separately for each morphology. Nevertheless, for reef-building corals the number of morphologies is much smaller than the number of species in an assemblage. Estimating demographic rates for each morphology individually is feasible, whereas estimating demographic rates for each species individually is not. Furthermore, it might be possible to measure morphology as a continuous variable at the level of the individual. Given the importance of colony morphology as a predictor of numerous demographic rates this is an important area of future research.

The strong differences in the individual components of colony fecundity, especially in the relationship of polyp maturity with colony size and in the number of oocytes per mature

polyp, indicate differences in evolutionary strategies even between species of the same morphology. For example, delayed maturity is predicted to result in higher initial growth rates and lower juvenile mortality when compared to early maturity (Stearns 1992). These differences in the individual components of fecundity may have important implications in the lifetime reproductive success.

In many systems, linking functional traits to demographic rates and their responses to abiotic and biotic variables has enhanced our understanding of patterns and processes in ecosystem function, and the maintenance of functional and species diversity (Angert et al. 2009, Lasky et al. 2014, Becerra 2015). In species-rich systems, biodiversity can be maintained via contributions from many different mechanisms; however, for reef corals, our assessment of the relative importance of these possible mechanisms has been hampered by the qualitative nature of our understanding of demographic trade-offs. The contributions of different coexistence-promoting mechanisms can be assessed by calibrating community dynamics models at the whole-population level and comparing species' fitness in the presence and absence of the mechanism (Adler et al. 2013). To do this, estimates of the relationships between demographic rates are needed. By quantitatively characterizing the relationship between fecundity and mechanical vulnerability and their interaction with colony size, I provide a foundation for investigating coexistence-promoting mechanisms in reef-corals. Similarly, high species richness, and the large number of rare species of corals, precludes the use of species-by-species projections of assemblage-scale effects of anthropogenic environmental change. Species within growth forms exhibit very similar constellations of demographic traits, but these constellations change substantially as colonies grow, and they differ markedly among growth forms. These findings indicate that projections of assemblage-scale effects of environmental change should prioritize the explicit

incorporation of size-structured dynamics of different growth forms over species-level taxonomic resolution.

Chapter 3: The effect of competition on coral colony growth and the relationship of competitive ability and demographic rates

3.1 Introduction

The effect of competition on individuals' fitness can affect community structure and dynamics. Competition occurs when two individuals consume common limiting resources, and it can reduce individual fitness by reducing the resource to sub-optimal levels (exploitation competition) or by reducing the competitor's access to the resource (interference competition). If one of the competitors is more efficient at exploiting the resource, competition can result in the local extinction of the weaker competitor (Gause 1934, Tilman 1982). Even when extinction does not occur, manipulative studies that have removed dominant species show that the subordinate species usually occupies areas that were previously occupied by the superior competitor (Paine 1966, Martin and Martin 2001). The energetic cost of competition can result in reductions in growth, fecundity or maintenance at the individual level, and the joint effect of competition on individuals in a community influences community structure (e.g., barnacles: Connell 1961; sea stars and mussel: Paine 1966; birds: Martin and Martin 2001). Understanding the effects of competition at the individual level is therefore necessary to predict changes in community composition.

Competition among benthic organisms for space can influence species abundance and richness (Chadwick and Morrow 2011). For corals, space is the main limiting resource and the capture of space provides access to other resources, such as nutrients and light. Competitive interactions among established adult colonies tend to be complex for various reasons. First, coral colonies can compete against each other through direct-contact

competition by digesting or overgrowing competitors, or without direct contact through overtopping (Figure 3.1-a). Taxa and colony morphologies that are good competitors in direct-contact competition tend to lose in overtopping competition and vice-versa (Lang and Chornesky 1990). Secondly, species competitive rankings are not strictly hierarchical and competitive outcomes are often inconsistent and can reverse over time (Lang and Chornesky 1990, Bak et al. 1982, Precoda et al. 2017). Additionally, size asymmetry between competitors influences competitive outcomes, favouring colonies of larger size (Zilberberg and Edmunds 2001). Competitive outcomes are therefore difficult to predict.

Competition among adult colonies generally results in inferior demographic rates. For example, colony growth is reduced when in competition against other corals (Romano 1990, Tanner 1997) or against algae (Tanner 1995, Lirman 2001, Box and Mumby 2007, *but see* Jompa and McCook 2002, Lapid and Chadwick 2006). However, studies that manipulate competition often create extremely high levels of competition (e.g., by fastening colonies to one another), which are only true for a small subset of competitive interactions. Additionally, in the central Indo-Pacific, assemblages are often species-rich with many different colony morphologies. In particular, there are numerous rapidly-growing branching species that compete through overtopping. Consequently, overtopping rather than direct-contact competition might be the dominant competitive mechanism on most reefs (Sheppard 1979). The effect of competition between coral colonies on colony growth under such natural conditions remains poorly understood.

Competitive abilities are commonly linked to traits (e.g. in plants: Goldberg and Landa 1991), and trade-offs can arise when traits favouring competitive abilities come at a cost to other ecological functions. Trade-offs between competitive ability, stress tolerance, tolerance to disturbance and reproductive output have long been proposed (MacArthur and Wilson 1967, Grime 1979) and are evident in various organisms (e.g. *fish:* Dunson and

Travis 1991; *plants:* Angert et al. 2009; *molluscs:* Krassoi et al. 2008). For scleractinian corals, colony morphology is recognised as an important trait affecting competitive ability (Precoda et al. 2017, Lang 1973, Connell et al. 2004), and demographic rates differ between different colony morphologies (Madin et al. 2014, Álvarez-Noriega et al. 2016 [Chapter 2 of this thesis], Dornelas et al. 2017). Colony morphology is highly correlated with colony growth (Dornelas et al. 2017), and fast growth rates should lead to victory in most overtopping encounters; in contrast, massive competitors are more aggressive in direct-contact competition (Lang 1973).

Trade-offs can arise if high competitive abilities are linked to inferior demographic rates in some colony morphologies or species. Trade-offs between competitive abilities and important demographic rates might prevent the best competitors from displacing subordinate species. However, for overtopping competition, competitively superior species often have higher growth rates than competitively inferior species; at least in some areas of the reef (Connell et al. 2004). In scleractinian corals, the relationships between competitive ability and other demographic rates are yet to be quantified.

Spatial arrangements in the community determine which individuals compete against each other, and can have important implications for community dynamics (Levins and Culver 1971, Tilman 1994). Aggregation of dominant conspecifics benefits subordinate species by increasing the number of intraspecific competitive encounters relative to interspecific ones, and thereby reducing competitive encounters between dominants and subordinates (Harper 1977) and reducing interspecific competition overall (Klopfer and Ives 1997). Spatial aggregation of conspecifics can facilitate coexistence under some circumstances, even though it is not a coexistence-promoting mechanism itself (Chesson and Neuhauser 2002). For example, in species with planktonic dispersal, coexistence is promoted when the dominant competitor forms conspecific clusters at settlement, leaving patches of free space where

inferior competitors can establish (Bolker and Pacala 1997). On coral reefs, some species form conspecific aggregations (Chadwick and Morrow 2011; Sheppard 1980), and abundant species tend to be more aggregated than rare species (Karlson et al. 2007), a pattern also observed in plants (He et al. 1997). If, as a result, superior competitors in coral assemblages experience elevated intraspecific competition, then coexistence with weaker competitors might be promoted.

Here, I first quantify the change in coral colony growth caused by competition, and I test whether species (or colony morphologies) differ in their competitive abilities depending on the type of competition. I then investigate the relationship between species' competitive abilities and colony fecundity, growth and susceptibility to mechanical dislodgement. I hypothesise that: 1) colonies experiencing more competition will grow at a slower rate than colonies experiencing less competition; 2) competitive outcomes depend on colony morphology and type of competition (direct-contact or overtopping); 3) colonies are more likely to compete with a colony of the same morphology than expected by chance; and 4) trade-offs emerge between competitive ability and at least one other demographic rate.

3.2 Methods

3.2.1 Study location and data collection

Data were collected on the semi-exposed reef crest of Lizard Island in the north of the Great Barrier Reef (GBR; 14.699839° S, 145.448674° E). In 2008, 30 colonies from each of 11 species belonging to five morphologies were tagged (depth ranging from 1-2m): arborescent (*A. intermedia* and arborescent encrusting: *Acropora robusta*), corymbose (*A. nasuta, A. millepora* and *A. spathulata*), digitate (*A. humilis* and *A. cf. digitifera*), massive (*Goniastrea pectinata* and *G. retiformis*), and tabular (*Acropora cytherea* and *A. hyacinthus*). For each

species, an effort was made to collect colonies from the entire range of colony sizes found at the site, without regard to the amount of competition they were experiencing *(see* Fig. B.1). Thus, I expect competition levels in the samples to be representative of competition levels experienced by each species at the study site. Coral cover on the reef crest was estimated using 10 by 10 m line intercept transects in 2011 at 40 ± 3.0 % (mean ± SE). The colonies were followed through time, and photographed from above with a scale plate every year from 2009 to 2013 (Madin et al. 2014, Álvarez-Noriega et al. 2016 [Chapter 2 of this thesis], Dornelas et al. 2017).

The photographs were corrected for barrel distortion, and the perimeters of the focal colonies were digitally traced to estimate colony area (planar area) and colony perimeter using ImageJ (Bethesda, Maryland, USA). Additionally, I marked the starting and ending points of contact in a competitive interaction on top of the digital image of the colony's perimeter, to measure the proportion of the colony's periphery involved in competitive interactions. I classified the competitive contacts as overtopping, digestion or overgrowth. An encounter was scored as overtopping when either the focal colony or a neighbour were partially covering the other colony on the planar view (Fig. 3.1-a and b). Colonies can also digest nearby colonies that are within the reach of their extruded mesenterial filaments, leaving a white border or injury in the area of contact (Lang 1973). An encounter was scored as digestion when either colony had a white border or injury near the margin of another colony (Fig. 3.1-c and d). An encounter was scored as overgrowth if one of the colonies was growing on the surface of the other colony (Fig. 3.1-e and f). Encounters scored as digestion or overgrowth were grouped together as 'direct-contact' encounters because there were few observations of both competitive mechanisms. Interactions were not considered competitive when colonies were in close proximity but with no signs of digestion, overgrowth or overtopping (i.e. standoffs). Growth was estimated as the change in colony planar area

between consecutive years on a log-scale (log[area in cm^2 at time $t+1$] – log[area in cm^2 at time t]). Change in planar area is a common measurement for growth because it represents the amount of space (the potentially limiting resource) acquired by an organism in an interval of time (e.g. Connell et al. 1997; Connell et al. 2004). Measuring growth as a change in planar area fails to account for vertical growth (Pratchett et al. 2015), which is particularly common in massive species (Lough and Barnes 2000). Thus, if growth in planar area decreases in response to competition, it could be due either to reduced growth overall, or redirection of growth in a vertical direction.

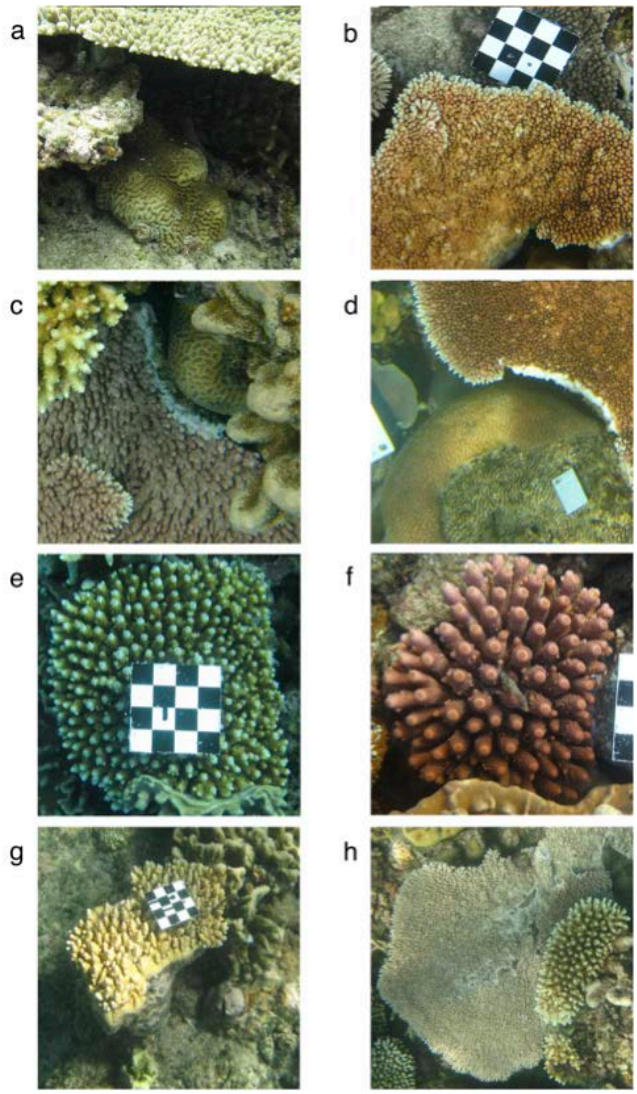

Figure 3.1 Photographs of competing colonies. (a, b) Tabular colonies overtopping competitors. (c, d) Tabular colonies being digested by massive neighbours. (e, f) A corymbose and a digitate colony being overgrown by a soft coral. (g, h) Elevated microhabitats of digitate colonies.

3.2.2 Statistical analysis

Effect of competition on growth:

I fitted a linear quantile regression to estimate colony growth as a function of colony size, species, competition (as the proportion of the colony's periphery in competition) and the interaction between species and competition. From this main model, I fitted subsequent models with each possible combination of a subset of explanatory variables, and the best-fit model was selected using Akaike weights (from the package 'qpcR'; Spies 2015). Following Dornelas et al. (2017), each set of models was fitted through the 95th, 50th and 5th quantile of colony growth. The 95th quantile captures the growth of the fastest-growing colonies (which I take to represent colonies in optimal conditions, i.e. maximum potential growth). Conversely, the 5th quantile captures the slowest-growing (often shrinking) colonies, which I take to represent colonies exposed to the highest levels of partial colony mortality. The 50th quantile is the median growth, which I take to represent growth under typical conditions and levels of natural mortality. It seems unlikely that winning overtopping competitive encounters (i.e., successfully overtopping another colony) would negatively affect colony growth of the winner. Therefore, I measured competition as the proportion of the focal colony's periphery being overtopped or in a direct-contact competitive encounter. Qualitative results were unchanged when standoffs were included in the analysis. Only a subset of models was fitted through quantiles 95th and 5th due to problems with convergence. The models were fitted using the R-package 'quantreg' (Koenker et al 2017).

Predictability of competitive outcomes:

I used a binomial regression to predict the probability of winning an overtopping encounter for each species (using the package 'rstanarm'; Stan Development Team 2016). Since each tagged colony could have up to five observations (one per year), I included colony identity as a random intercept (with the function 'stan_glmer'). Similarly, I fitted another binomial regression to predict the probability of winning a direct-contact competitive encounter with

species as the explanatory variable and again with colony identity as a random intercept. To test the effect of colony identity on the outcome of competitive interactions, I fitted two more binomial regressions: one for overtopping interactions and one for direct-contact competitive interactions, this time without colony identity as a random intercept (with the function 'stan_glm'). I compared the models with and without colony identity using leave-one-out cross-validation, and calculating the difference in the expected log predictive density (ELPD) of the models and the standard error associated with this difference (Vehtari et al. 2016). A negative ELPD indicates that the expected predictive accuracy of the first model is higher than that of the second one. A better fit of the model with colony identity as a random effect compared to the model without colony identity would indicate that the competitive outcomes for individual colonies were consistent among competitors and through time (i.e. if a colony was winning against one competitor at time *t*, it is disproportionately likely that it will also be winning against other competitors, and at other times. I would expect such a pattern if, for instance, a colony's position on the reef, or its height relative to its planar area, gave it a competitive edge. I identified competitors to genus level, but I later grouped competitors according to their colony morphologies due to low replication in most genera. Only coral-coral interactions were included, since interactions with macroalgae and sponges were rare.

Intraspecific vs. interspecific competition:

I used a generalised linear model with a binomial error structure to predict the probability of a competitive interaction being with another colony of the same morphology. The response variable was the competitor's morphology (same as focal colony's or different). I did this analysis separately for each focal morphology.

Relationship between performance in overtopping competition and demographic rates:

Given that overtopping competition was commonly observed and direct-contact competition was rare, I used the species' performance in overtopping competition as a proxy for

competitive ability. I used a non-parametric Spearman's rank correlation ρ to test for a correlation between the probability of winning a competitive encounter that involves overtopping and four demographic rates: colony growth, mechanical vulnerability, reproductive investment, and number of oocytes per colony at the species level. Mechanical vulnerability was measured by the colony shape factor (CSF; Madin and Connolly 2006), which is a dimensionless quantity that depends on colony size and colony shape. An increase in CSF corresponds to an increase in mechanical vulnerability. CSF values decrease with increasing colony base width (i.e., bottom-heavy) and increase with increasing colony width above the base (i.e., top-heavy). I estimated CSF values for the largest colonies observed in this study using the CSF regressions in Madin et al. (2014). Reproductive investment and number of oocytes per colony are proxies for colony fecundity. Reproductive investment takes into account the estimated number of oocytes produced per colony and their energy (carbon) content. I estimated reproductive investment and number of oocytes from regressions of reproductive investment versus colony sizes and of number of oocytes versus colony size in Álvarez-Noriega et al. (2016) [Chapter 2 of this thesis] for the range of observed colony sizes, and I calculated the mean values for each proxy. Note that regressions were only available for eight out of the 11 species in this study, and that fecundity measurements were taken at the site but from different colonies than those in this study, because sampling for fecundity in corals is destructive (branches must be broken off of the colony) and such injuries can affect subsequent colony growth.

To account for differences between *Acropora* and *Goniastrea* species, I tested the correlation between the probability of winning an overtopping competitive encounter and the demographic rates with all species, and then again only for the *Acropora* species. All analyses were performed in R (R Core Team 2016).

3.3 Results

Although competition was an explanatory variable in the best-fit models predicting colony growth (Table B.1), competition did not significantly reduce potential colony growth, realized net colony growth or growth under severe partial mortality (Table 3.1). *Acropora* species are more likely to win a competitive encounter that involves overtopping, regardless of their colony growth form, whereas *Goniastrea* species are not (Fig. 3.2-a), but their probability of winning a direct-contact competitive encounter is generally low (Fig. 3.2-b). In contrast, *Goniastrea* species perform poorly in overtopping competition (Fig. 3.2-a), but have very high probabilities of winning in direct-contact competition (Fig. 3.2-b). Overtopping was the most prevalent type of competition, being over 7 times more common than direct-contact competitive encounters (2045 vs. 275 competitive encounters observed). Most of the 11 species had overtopping interactions with all competitor groups (Fig. 3.2-a), while direct-contact interactions mostly occurred with only a subset of competitor groups for most species (Fig. 3.2-b), possibly due to the lower number of direct-contact interactions. For example, *G. pectinata* competed with all competitor groups by being overtopped, but it competed directly only with tabular *Acropora* species.

Table 3.1. Coefficient estimates of the best-fit models predicting the 5th, 50th, and 95th quantiles of colony growth with quantile regression. Standard errors were computed using bootstrapping techniques. Bold letters indicate the significant effects for each regression.

	quantile 0.05			
	coefficient	SE	t value	Pr(>|t|)
intercept	**-0.704**	**0.214**	**-3.290**	**0.001**
log (area)	0.016	0.030	0.543	0.588
competition	0.284	0.154	1.842	0.066

	quantile 0.50			
	coefficient	SE	t value	Pr(>|t|)
intercept	**0.401**	**0.093**	**4.326**	**<0.001**
log (area)	**-0.076**	**0.014**	**-5.447**	**<0.001**
competition	0.186	0.198	0.939	0.348

	quantile 0.95			
	coefficient	SE	t value	Pr(>|t|)
intercept	**2.319**	**0.522**	**4.440**	**<0.001**
log (area)	**-0.252**	**0.069**	**-3.645**	**<0.001**
competition	-0.415	0.545	-0.761	0.447

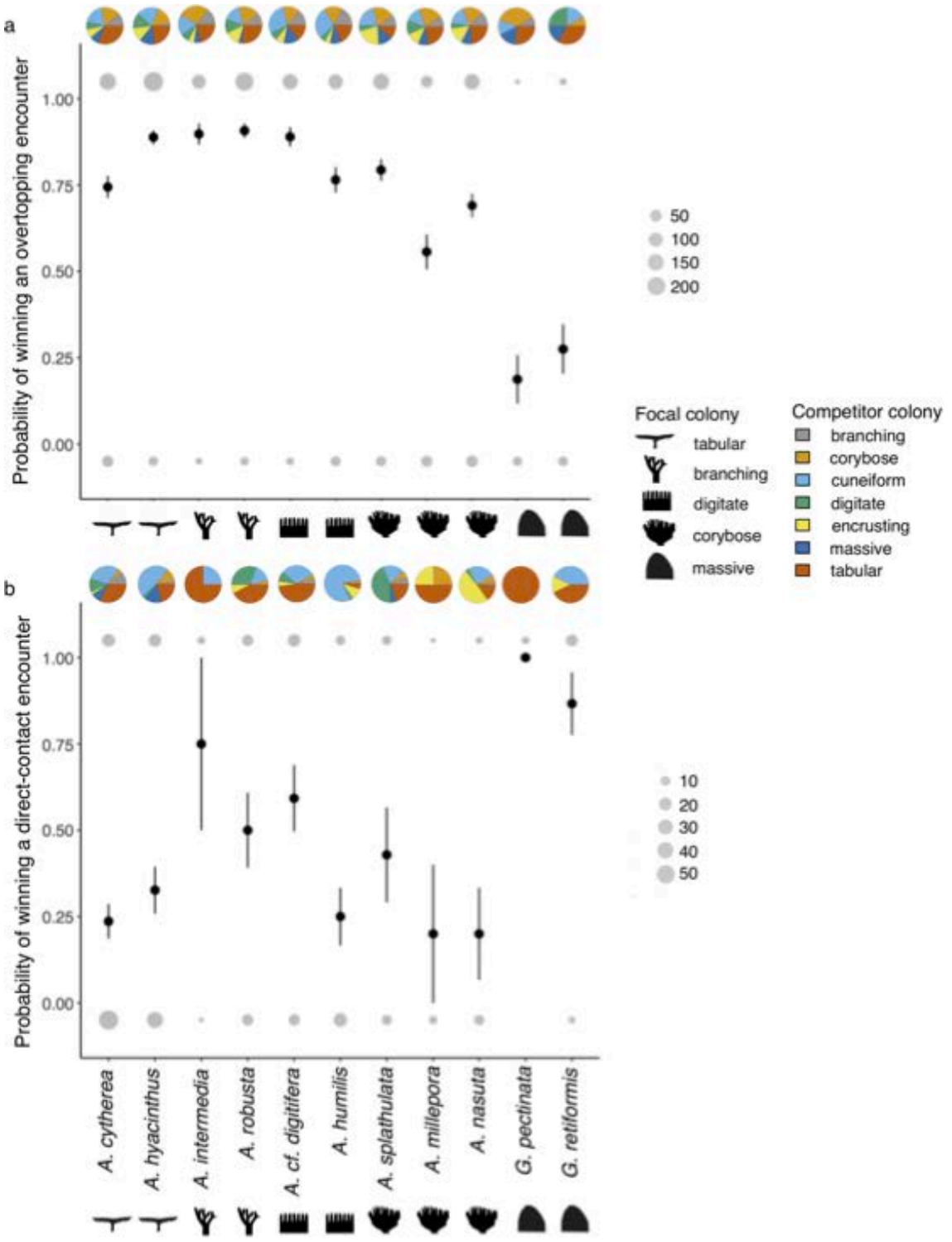

Figure 3.2. Probability of winning competitive encounters. (a) Probability of winning an overtopping competitive encounter for each species. (b) Probability of winning a direct-contact competitive encounter for each species. Line ranges indicate standard errors. The pie charts show the distribution of the competitors' colony morphology. The grey points correspond to the data and their size is proportional to the number of observations. Note that their size represents different number of counts for the probability of winning an overtopping competitive encounter and for the probability of winning a direct-contact competitive encounter. Points were displaced slightly below 0 (for encounters lost) and slightly above 1 (for encounters won) to avoid overlap with estimates and credible intervals.

Colony identity was an important factor determining overtopping competitive outcomes only. Colonies tended to be more consistently “winners” or “losers” in overtopping encounters than the estimated average for the species. In contrast, there was no colony-level random effect in the outcome of direct-contact encounters (i.e. colonies did not tend to be more consistently winners or losers than average for their species). The difference in expected log predictive density (ELPD) between the model with colony identity as a random effect and the model without random effects for overtopping competition was -61.8 ± 11.6, indicating that the first model had a better fit than the second one. In contrast, for direct-contact competition the best fit did not include colony identity as a random effect (ELPD: 16.9±11.5).

Colonies that were good overtoppers were also fast growing (Fig. 3.3- a), vulnerable to dislodgement (Fig. 3.3-b) and highly fecund (Fig. 3.3-c, d). However, the correlation was only significant between overtopping, mechanical vulnerability (CSF) and maximum reproductive investment were only significant when including the *Goniastrea* species (Table 3.2).

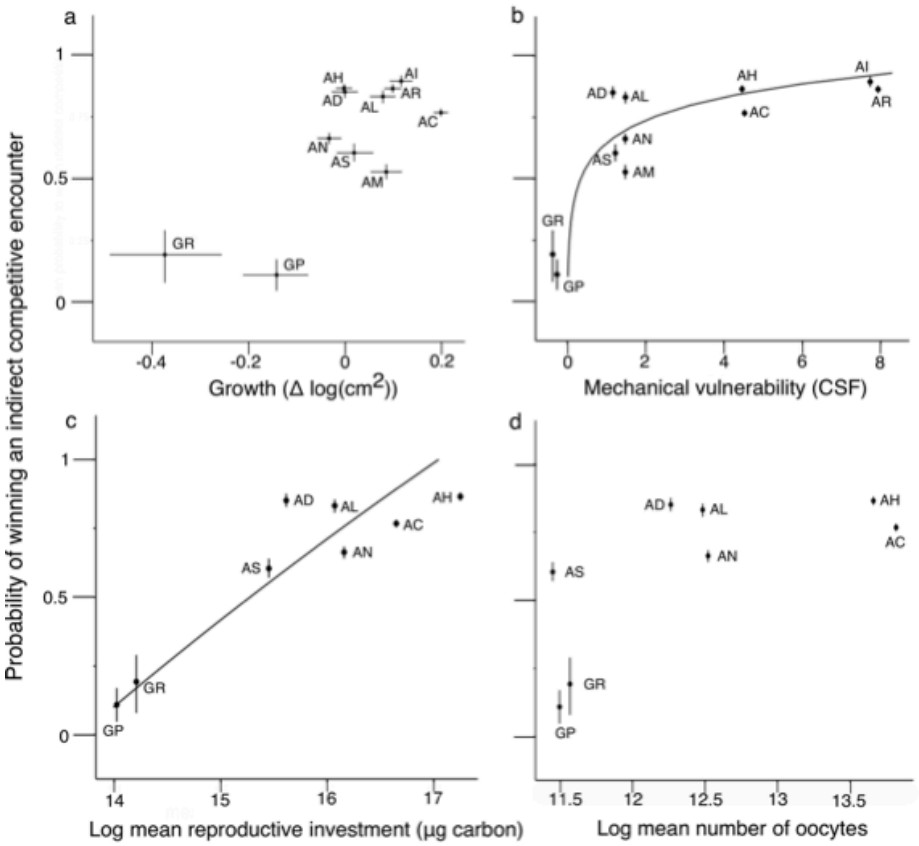

Figure 3.3 Relationships between overtopping competitive ability and key demographic traits. (a) Mean colony growth rate [log(area in cm2 at time t + 1)/log(area in cm2 at time t)] vs. the probability of winning an overtopping competitive encounter. (b) Mechanical vulnerability (CSF) of the largest colonies vs. the probability of winning an overtopping competitive encounter. (c) Mean reproductive energy investment per colony (carbon content in µg; log-scale) vs. the probability of winning an overtopping competitive encounter. (d) Mean number of oocytes per colony (log-scale) vs. the probability of winning an overtopping competitive encounter. The line range and domain correspond to the 95% credible intervals. Labels indicate species (GR- *G. retiformis*, GP- *G. pectinata*, AN- *A. nasuta*, AS- *A. humilis*, AM- *A. millepora*, AD- *A. cf. digitifera*, AL- *A. spathulata*, AC- *A. cytherea*, AH- *A. hyacinthus*, AR- *A. robusta*, and AI- *A. intermedia*). Lines show the fitted inverse exponential functions when the correlation is significant.

Table 3.2. Spearman's rank correlation results for the relationships between the different demographic rates and the mean probability of winning an overtopping competitive encounter, first including the two *Goniastrea* species and then with *Acropora* species only.

	Including *Goniastrea* spp.		*Acropora* spp. only	
	p-value	ρ	p-value	ρ
growth vs. overtopping probability	0.107	0.518	0.744	0.133
CSF vs. overtopping probability	0.010	0.755	0.121	0.567
reproductive investment vs. overtopping probability	0.028	0.782	0.356	0.486
number of oocytes vs. overtopping probability	0.096	0.643	0.564	0.314

Tabular colonies were disproportionally more likely to compete with other tabular colonies than with colonies of other morphologies, but other morphologies did not compete disproportionately with colonies of the same morphology (Fig. 3.4, Table B.2).

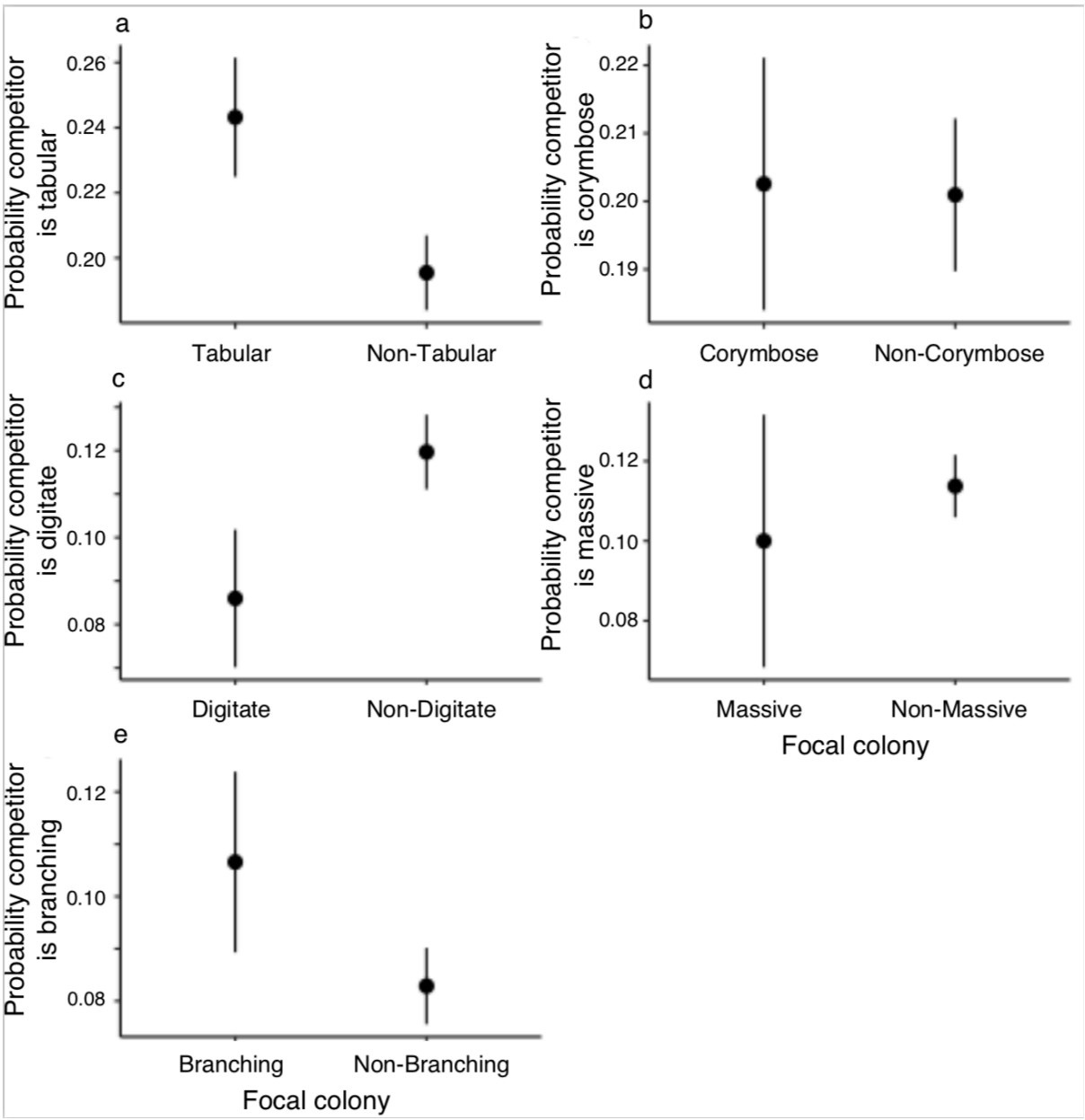

Figure 3.4. Intra- vs. inter-morphological group competition. (a) Probability of a competitor having a tabular morphology if the focal colony has a tabular morphology vs. other morphology. (b) Probability of a competitor having a corymbose morphology if the focal colony has a corymbose morphology vs. other morphology. (c) Probability of a competitor having a digitate morphology if the focal colony has a digitate morphology vs. other morphology. (d) Probability of a competitor having a massive morphology if the focal colony has a massive morphology vs. other morphology. (e) Probability of a competitor having a branching morphology if the focal colony has a branching morphology vs. other morphology. Line ranges indicate standard errors.

3.4 Discussion

Despite previous findings showing a reduction in growth with competition for at least some species (Romano 1990, Tanner 1997, Karlson 1978) competition between corals did not reduce colony growth on the reef crest of Lizard Island on the GBR. The intensity of competition is likely to be affected by many factors, in particular coral cover. Competitive encounters are likely to be more frequent at a higher coral cover because there is a greater chance of colonies' edges overlapping. Additionally, competition levels also fluctuate through time, being less intense shortly after a major disturbance and more intense as populations recover. Coral cover at the study site on Lizard Island at mean of 40 ± 3.0 % was considerably higher than the mean of 29% on reef crest along the length of the Great Barrier Reef between 1995 and 2009 (Osborne et al. 2011). While the data set only captures a five-year window of the successional sequence of competition levels, given the relatively high level of coral cover, it is likely that competition in this study is more intense than its temporal average. The lack of an effect of competition on growth does not necessarily imply that competition has no role in community dynamics. For example, competition might negatively affect demographic rates other than growth, such as reproduction (*but see* Tanner 1997) or survivorship, particularly if competing colonies are maintaining growth at the cost of lower skeletal density and therefore great susceptibility to mechanical disturbance. Furthermore, competition for space can also occur between adult colonies and recruits via pre-emption of space by adults, and among recruits. I hypothesise that competition among these life history stages affect community dynamics more strongly than competition among adults, particularly since recruitment success fluctuates idiosyncratically (Hughes et al. 1999, Adjeroud et al. 2007).

The competitive performance of corals was consistent among corals of the same genus. Good performance by corals in one type of competition came at the cost of performance in the other type of competition. That is, *Acropora* colonies had high probability of winning an overtopping interaction but also high probability of losing a direct-contact interaction, and the opposite was true for *Goniastrea* species. Surprisingly, there were no clear differences among *Acropora* colony morphologies. Considering that branching and tabular colonies have branches that extend much farther out from the base than digitate and corymbose colonies, I expected that the former would be better overtoppers than the latter. This counter-intuitive result can be partially explained for digitate colonies by their microhabitat: they were commonly located on elevated areas of the reef crest and would commonly grow and extend out into the water column (Fig. 3.1-g and h).

In contrast to coral assemblages with very low abundances of *Acropora*, where digestion is the most common type of interaction (e.g. the Caribbean: Lang 1973; Gulf of Mexico: Ferriz-Domínguez and Horta-Puga 2001), overtopping competition is vastly more prevalent than direct-contact competition at the site on Lizard Island, GBR. Consequently, fast-growing *Acropora* spp. with complex colony morphologies had a competitive advantage over their competitors, whereas slow-growing massive *Goniastrea* spp. did not. However, as indicated by the better fit of the model with colony identity as a random effect, indirect competitive outcomes were affected by the particular conditions of individual colonies: some colonies were consistently more likely than average for their species to be successfully overtopping their competitors, while other colonies of the same species were less likely than average to be overtopping their competitors. Such differences among colonies of the same species could represent differences in position on the reef (e.g., frequent winners might be growing on substrate that is slightly elevated, relative to the surrounding substrate), or

differences in colony shape (e.g., frequent winners are somewhat taller than average, given their size).

Tabular colonies were more likely to compete against conspecifics than expected by chance. Tabular colonies grow fast (Dornelas et al. 2017) and can kill conspecifics placed in their shade (Baird and Hughes 2000) and sometimes dominate large areas of the reef, forming low-diversity zones (Done 1982). Aggregation of superior competitors can allow inferior competitors to persist in the community by leaving free space to colonize or rapidly exploit if there is a trade-off between competition and colonization or between competition and rapid exploitation (Bolker and Pacala 1997). However, the negligible effect of competition on growth suggests that aggregation of competitive dominants is unlikely to promote persistence of inferior competitors by increasing intraspecific relative to interspecific competition between adult colonies (*but see* Idjadi and Karlson 2007). Nevertheless, aggregation of conspecific dominants could be coexistence-promoting through competition between adults and recruits (Baird and Hughes 2000, Vermeij 2005, Marhaver et al. 2013). Furthermore, if settlement processes produce aggregations of superior competitors, conspecific settlers might suffer density-dependent mortality (Vermeij et al. 2009, Doropoulos et al. 2017) that will limit population growth.

Good performance in overtopping competition was associated with higher mechanical instability. Trade-offs are important because they can reduce differences in fitness between competitors (Chesson 2000a), and thereby promote or maintain species richness. For example, branching colonies have high probabilities of overtopping massive colonies but they are also more easily dislodged by strong wave action, which then releases massive colonies from competition. The trade-off between competitive abilities and mechanical stability in corals has long been proposed (Connell 1978), but not tested. However, this trade-off may not have important consequences at the assemblage level if the amount of

competition experienced in the field does not materially affect colonies' demographic rates. Although the trade-off between competition and mechanical stability was only significant when including *Goniastrea* species, a moderate positive relationship was still present when only the *Acropora* species were included, and it would be interesting to test if the trade-off holds when including a broader range of taxa. In contrast to the negative relationship between overtopping competitive ability and mechanical stability, the positive relationship between overtopping competitive ability and reproductive investment means that the best competitors also invest the most in reproduction, thereby increasing differences in fitness between species. While this relationship holds at the species level, it is possible that individual colonies reduce investment into reproduction in the presence of competition. The positive relationship between overtopping competitive ability and reproductive investment diverges from traditional plant ecology, where fast growth and high fecundity are typically associated with 'weedy', or 'ruderal', life-history strategies, which are also characterised by poor competitive ability (Grime 1979).

Competition is typically thought to be one of the major factors limiting population growth and shaping community structure. Here, results show that adult growth is density-independent for realistic levels of crowding in coral assemblages- a system where competition is typically thought to be important. Additionally, results show that there is a trade-off between overtopping and direct-contact competitive abilities, but competitive outcomes depend on the particular conditions of competitors. The absence of an absolute competitive dominant and the lack of a negative effect of competition on an important demographic rate suggest that that competition between adults is less likely to influence coral community dynamics than previously thought, and that density-dependent processes like competition may be more important at other life-stages of corals.

Chapter 4: Disturbance-induced relative nonlinearity of competition promotes coexistence in reef-building corals

4.1 Introduction

Reef-building coral assemblages are an example of the 'paradox of the plankton' (Hutchinson 1961): they can be very species-rich (Veron et al. 2011), even though all species compete for the same, small number of limiting resources: space, and access to light and nutrients in the water column. However, the processes maintaining these levels of biodiversity remain enigmatic. A classical explanation for reef coral coexistence involves a trade-off between competitive ability and susceptibility to disturbance: corals that are susceptible to disturbance are also dominant competitors with the capacity to overtop and displace other species in the absence of disturbance (Connell 1978). However, the ecological models that produce such tradeoff-based coexistence require that the dominant competitor be able to displace adults of the subordinate competitor (Levins and Culver 1971, Connolly and Muko 2003). While corals do differ in competitive ability (Lang and Chornesky 1990), any such displacement effect is likely to be very weak if present at all for indirect competitive encounters such as overtopping, unless coral cover is extremely high (Álvarez-Noriega et al. 2018 [Chapter 3 of this thesis]).

An alternative hypothesis is that biodiversity is maintained by neutral dynamics, according to which variation in species' abundances is due purely to demographic stochasticity (chance variation in fates of individuals), and biodiversity is maintained through a balance of immigration or speciation and extinction (Hubbell 2001). However, neutral models cannot capture the high heterogeneity in relative abundances among species

(Connolly et al. 2009, 2014, 2017), nor patterns of community similarity (Dornelas et al. 2006).

In some systems, environmental variation plays a major role in species coexistence (e.g. zooplankton: Cáceres 1997; freshwater diatoms: Descamps-Julien and González 2005; annual plants: Angert et al. 2009). Community dynamics that are strongly influenced by environmental conditions are predicted to change in the near future due to climate change (Huxman et al. 2013). Coexistence-promoting mechanisms that depend on population fluctuations (i.e. fluctuation-dependent mechanisms) are commonly driven by fluctuations in environmental conditions affecting demographic rates (Chesson 2000a). Quantifying the contribution of the fluctuation-dependent mechanisms to species coexistence has received increasing attention in recent years (e.g. Yuan and Chesson 2015, Ellner et al. 2016) and may serve as a base to predict how communities will respond to environmental change (Miller et al. 2011). Fluctuation-dependent coexistence mechanisms fall into two main categories: the storage effect (Chesson and Warner 1981) and relative nonlinearity of competition (Armstrong and McGehee 1980). Chesson (1994) developed the theoretical background to quantify the contributions of the storage effect and relative nonlinearity in species coexistence.

Relative nonlinearity of competition is a coexistence-promoting mechanism in which each competitor performs best at a different resource level. This is possible when competitors differ in the shape (i.e. nonlinearity) of their response to a limiting factor, and the limiting factor fluctuates between levels that favour one competitor, and levels that favour its opponent. Following Jensen's inequality (Jensen 1906), the average of the population growth (r) as a function of a limiting factor R ($\overline{r(R)}$) is different to r evaluated at the mean of the limiting factor ($r(\bar{R})$). If the relationship between r and R is convex, then $\overline{r(R)} \geq r(\bar{R})$, otherwise $\overline{r(R)} \leq r(\bar{R})$, which means that nonlinearities in the dependence of a common

limiting factor can either boost or depress competitors' growth rates, relative to a constant environment at mean resource levels. Relative nonlinearity promotes coexistence when it boosts population growth of the inferior competitor but does not depress the superior competitor's population growth too strongly (Chesson 1994). Additionally, the species that benefits more from fluctuations in the limiting factor must reduce these fluctuations when it is a resident, and the species that is less benefited by fluctuations must increase them when it is a resident. In that way, when each species is abundant, it produces conditions that favour its competitor.

The storage effect is a coexistence-promoting mechanism where benefits gained during favourable times are 'stored', allowing species to persist through unfavourable times. For this mechanism to operate, species must differ in their response to the environment, and there must be an interaction between competition and environmental conditions (Chesson 2000a). The population growth rate of the invader species must be less affected by competition when it experiences an unfavourable environment than when it experiences a favourable environment (i.e. the interaction between the environment and competition must be subadditive). Additionally, the resident species must suffer strong competition when it experiences a favourable environment, therefore limiting its own growth. Uncorrelated (or negatively correlated) responses to the environment mean that the invader species can take advantage of years that are favourable to it because, since the resident species does not experience a favourable environment, overall competition is lower.

Disturbance is a source of environmental variation that can influence coexistence through fluctuation-mediated mechanisms (Shea et al. 2004; Miller and Chesson 2009). Responses to disturbance and post-disturbance recovery can be species-specific, depending on trait values that influence susceptibility. For example, below-ground-nesting bee species are more negatively affected by tilling than above-ground nesting species, and the opposite is

true for intensive agricultural land use (Williams et al. 2010). Additionally, susceptibility to disturbance can differ among life-stages or sizes (e.g. in trees, Herault et al. 2010; in corals, Madin and Connolly 2006). Interactions between life-stages (or sizes) and environmental conditions have the potential to buffer population growth (Tredennick et al. 2018). In corals, the size-dependent response to mechanical disturbance (i.e. wave action) differs among species with different colony morphologies (Madin and Connolly 2006), and mechanical disturbance has a strong effect on overall mortality patterns observed on the reef (Madin et al. 2014).

Fluctuation-dependent coexistence mechanisms have been invoked to explain maintenance of coral biodiversity (Dornelas et al. 2006), but whether and which environmental fluctuations on coral reefs are genuinely coexistence-promoting (i.e., whether they induce a storage effect or relative nonlinearity of competition) has yet to be demonstrated. Here, I analysed a model for competition between two coral populations in the presence of fluctuating, size-dependent mortality from wave action. I calibrated the model using demographic parameters from a 5-year data set collected on Lizard Island (GBR), with one population representing a species with a tabular growth form that becomes increasingly susceptible to dislodgment as it grows (Fig. 4.1-a), and the other population representing a digitate growth form that is more mechanically stable (Fig. 4.1-b). I analysed the model to determine whether differences in size-dependent susceptibility to wave action promote fluctuation-mediated coexistence between these two populations, and to quantify the contribution of relative nonlinearity to such coexistence.

Figure 4.1. Stylized illustration of tabular colonies (panel a) and digitate colonies (panel b).

4.2 Methods

4.2.1 *Competitors*

I examined coexistence between two coral populations, one with a tabular growth form, and the other with a digitate growth form. One of the most common tabular coral species is *Acropora hyacinthus*, which is often numerically dominant in reef-crest habitats throughout much of the Indo-Pacific (Stimson 1985, Baird and Hughes 2000). Nonetheless, the model population was also representative of other, less abundant tabular species (see *Parameter estimation*). The digitate species was based principally on the demography of *A. cf. digitifera*, but it was also representative of other digitate species that frequently co-occur on reef crests with tabular coral species (e.g., *A. humilis*). The demographic rates of each growth form were obtained by fitting size-dependent relationships to data from both species pooled within each growth form, and therefore these populations represented growth forms rather than particular species. I chose tabular corals because they exhibit strong size-dependent susceptibility to mechanical disturbance (e.g., Madin and Connolly 2006), and because, in the absence of hydrodynamic disturbances (i.e., severe storms and cyclones), they can monopolize space in reef crest and wave-exposed reef flat habitats (Connell et al. 1997, Baird and Hughes 2000). I chose digitate *Acropora* as the competitor population because this growth form is very

common in the wave-exposed habitats where tabular corals flourish (Done 1982, Dornelas and Connolly 2008).

4.2.2 *Model structure*

I used integral projection models (IPM; Easterling et al. 2000) to characterise community dynamics. IPMs are discrete-time models that use a continuous state variable to describe population dynamics. In reef corals, fecundity, growth and survival are functions of colony size (Hall and Hughes 1996, Pratchett et al. 2015, Hughes and Connell 1987), so I modelled the dynamics of the colony size distributions of the competing populations over time.

In the model, demographic processes over each year were divided into two sub-intervals: from time *t*-1 to time *t-h* (where $h \in [1 - z, 1)$ and $z \to 0$), when reproduction and larval settlement occurred, and 2) from time *t-h* to time *t*, when disturbance, growth, and survival occurred. In other words, reproduction occurred before growth and survival. During time step 1, corals reproduced, and the resulting larvae settled. Because coral recruitment is proportional to unoccupied space (Connell et al. 1997), I modelled the proportion of larvae successfully recruiting as depending linearly on free space availability $1 - \sum_{j=1}^{k} N_{j,t}$, where $N_{j,t}$ is the proportion of space occupied by species *j* at time *t*, and *k* is the number of competing species (two in my simulations). $N_{j,t}$ was calculated by integrating the density of colonies of size *y* at time *t* ($n_j(y,t)$) times their planar area, and then normalizing by the total habitat area (*A*):

$$N_{j,t} = \frac{\int y[n_j(y,t)]dy}{A}.$$

(Equation 4.1)

The density of colonies of size *x* at time *t-h* for species *j* ($n_j(x, t-h)$) was the sum of (i) the density of colonies size *x* just before settlement ($n_j(x, t-1)$) and (ii) the density of successful settlers of size *x* at time *t-h* produced through reproduction of colonies size *x* at

time *t*-1. The number of possible settlers was given by the integral of the fecundity kernel ($F_j(x, x')$) times the size distribution at time *t*-1 ($n_j(x, t-1)$). The fecundity kernel was a surface containing transitions from size *x* at time *t*-1 to size *x'* at time *t-h*, and thus it implicitly included reproductive output, larval survival, and successful settlement. Because coral settlement competence peaks 1-2 weeks after spawning, I assumed that mortality and growth of colonies already present at time *t*-1 occurs after this short sub-interval, in between settlement in one year and spawning in the next year. With the above assumptions, the density of successful settlers was:

$$R_j(x', t-h) = (1 - \sum_{i=1}^{k} N_{i,t-1}) \int_0^{\infty} F_j(x, x')\, n_j(x, t-1) dx.$$

(Equation 4.2)

The size distribution at time *t-h* was then:

$$n_j(x', t-h) = n_j(x', t-1) + R_j(x', t-h).$$

(Equation 4.3)

In the second sub interval (*t-h* to time *t*), the model predicted growth and survival of all corals (including those newly recruited) and the proportion of space occupied by each species was calculated (N_j). Survival from time *t-h* to time *t* ($S_{j,t-h}(x')$) had two components: a stochastic component that depends on susceptibility to the strongest yearly mechanical disturbance ($D_{j,t-h}(x')$), and a deterministic component that represents 'background' mortality ($M_j(x')$; i.e. mortality independent of mechanical disturbance):

$$S_{j,t-h}(x') = (1 - D_{j,t-h}(x'))\ (1 - M_j(x')).$$

(Equation 4.4)

The distribution of colonies of size *y* at time *t+1* depended on the survival of colonies of size *x* ($S_{j,t-h}(x)$) and their size-dependent growth to colony size *y* ($G_j(x, y)$) from time *t-h* to time *t:*

$$n_j(y,t) = \int_0^{\infty} [S_{j,t-h}(x') G_j(x', y)] n_j(x', t-h) dx'.$$

(Equation 4.5)

Growth was density-independent (see Álvarez-Noriega et al. 2018 [Chapter 3 of this thesis]) and was modelled as a linear function of size on a logarithmic scale ($\log(x') \sim \log(y)$).

4.2.3 *Parameter estimation*

Model parameters are reported in Table 4.1.

Growth, fecundity, and background mortality were obtained from a 5-yr data set of 30 colonies per species on the reef crest of Lizard Island, northern Great Barrier Reef (14.699839°S, 145.448674°E) (Madin et al. 2014, Álvarez-Noriega et al. 2016 [Chapter 2 of this thesis], Dornelas et al. 2017). For each growth form, demographic data of both species (*A. hyacinthus* and *A. cytherea* for tabular corals and *A. cf. digitifera* and *A. humilis* for digitate corals) were pooled for analysis.

The fecundity function ($F(x, x')$) depended on various components: the size-dependent probability of a polyp being mature (p_x), the size-dependent number of oocytes per mature polyp (m_x), the number of polyps per projected unit area (ρ), the projected area of the colony (w) and the settlement probability (q):

$$F(x, x') = p_x m_x \rho w q.$$

(Equation 4.6)

The settlement probability included the probability of an egg to be fertilised and become a larva, the probability of the larva to successfully settle. The probability of the larva to successfully settle can depend on larval density (i.e. there can be competition among larvae for settlement). However, there is experimental evidence indicating that larval mortality is density-independent and that per-capita settlement, if affected at all, is positively affected by higher larval densities (in the lab: Doropoulos et al. 2017, 2018; in the field: Heyward et al.

2002; Edwards et al. 2015). Consequently, I assumed no competition among larvae (i.e., successful recruitment depended on unoccupied space, but not on the density of offspring seeking to settle).

The number of polyps per projected unit area excluded the tip of the branches, which have young immature polyps (i.e. the sterile zone, Wallace 1985). All fecundity estimates except for settlement probability were obtained from Álvarez-Noriega et al. (2016) [Chapter 2 of this thesis]. Since there is no information available on settlement probability, I fixed a value resulting in coral cover about 50-60% of both morphologies in the absence of competitors, which was approximately the coral cover at the site when the demographic rates were estimated.

Mortality due to mechanical disturbance was determined by comparing each colony's 'Colony Shape Factor' (CSF) to the 'Dislodgment Mechanical Threshold' (DMT) imposed by the yearly maximum hydrodynamic disturbance. Both quantities were derived by Madin and Connolly (2006), who showed that colonies should be dislodged when CSF > DMT, and found good agreement of the threshold with field data. CSF is defined as:

$$\frac{16}{d_{\parallel}^2 d_{\perp} \pi} \int_{y=0}^{h} y\, w(y) dy,$$

(Equation 4.7)

Where $d_{\parallel}$ is the width of the base of the colony parallel to water flow and $d_{\perp}$ is the width of the base of the colony perpendicular to water flow. $w(y)$ is the width of the colony perpendicular to water flow as a function of y, which is the distance above the substrate. Colony height is represented by h. DMT is defined as:

$$\frac{\sigma_s}{U^2 \rho_w},$$

(Equation 4.8)

where σ_s is the tensile strength of the substrate ($\sim$2x10^5 N m^{-2} on Lizard Island), U is water velocity, and ρ_w is water density (1030 kg m^{-3}) (Madin and Connolly 2006).

In each year of the simulation, a random wind velocity was drawn from a gamma distribution (α=2.18, β=0.35), with parameters estimated from the distribution of a 37-year wind velocity data for the Low Isles (16.383°S, 145.567°E) (from the Australian Bureau of Meteorology), approximately 180 km south of Lizard Island (Madin et al. 2006). Wind data from Lizard Island was not used since it was only available from 2010 to 2017 (Australian Institute of Marine Science 2017). Water velocity at the reef crest as a function of wind velocity was estimated using wind and water velocity at the reef crest collected on the site (Madin et al. 2006). I predicted water velocity, *u*, as a saturating function of wind velocity, *v*, because wave energy is limited by fetch and depth:

$$u = a(1 - e^{-bv})$$

(Equation 4.9)

where *a* and *b* are fitted parameters, estimated by least-squares estimation (a= 5.10, b= 0.04; Appendix C1 Chapter 4). Using Madin et al. (2014)'s CSF regressions, colonies were predicted to dislodge if the DMT imposed by the yearly maximum wind velocity was smaller than the colony's estimated CSF (Madin and Connolly 2006). Colony dislodgement was assumed to cause colony mortality.

Background mortality (mortality independent of mechanical disturbance) was estimated from mortality data from 2009-2012 (Madin et al. 2014). CSF for each individual colony was estimated and compared to the maximum dislodgement mechanical threshold imposed by the environment that year (estimated from wind data at the site, Australian Institute of Marine Science 2017). As predicted by theory (Madin and Connolly 2006) and validated with mortality data on the reef (Madin et al. 2014), colonies that had CSF larger than the DMT estimated for that year were assumed to have been dislodged. Since dislodged colonies have very low survival rates (Smith and Hughes 1999), colonies predicted to dislodge were assumed dead and were eliminated from the data set. With the remaining data,

two linear models with a binomial error structure were fitted for each growth form: one with colony area as an explanatory variable (log-scale) and one independent of colony area. Models were compared using AIC, and the best-fit model for each growth form was used in the simulations (Appendix C2 Chapter 4).

Table 4.1. Model parameters.

$N_{j,t}$	proportion of space occupied by species *j* at time *t*
$n_j(y,t)$	density of colonies of species *j* size *y* at time *t*
A	total habitat area
$F_j(x,x'))$	fecundity function of species *j*
$R_j(x',t-h)$	density of successful settlers of species *j*
$S_{j,t-h}(x')$	survival of colonies size *x'* of species *j* from time *t-h* to time *t*
$D_{j,t-h}(x')$	mortality of colonies size *x'* of species *j* from time *t-h* to time *t* caused by mechanical disturbance
$M_j(x')$	mortality of colonies size *x'* of species *j* from time *t-h* to time *t* independent of mechanical disturbance
$G_j(x,y)$	growth function of species *j*
p_x	probability of a polyp being mature from a colony size *x*
m_x	number of oocytes per mature polyp of a colony size *x*
ρ	number of polyps per projected unit area
w	projected area of the colony
q	settlement probability

4.2.4 *Analysis of coexistence*

Here, I summarized my approach to quantifying coexistence mechanisms (for an extended explanation, see appendix C3 Chapter 4). The population growth rate ($r_j(t)$) can be expressed in terms of an environmentally dependent parameter ($E_j(t)$) and a competition parameter ($C_j(t)$). I defined $E_j(t)$ as the maximum population potential growth (i.e. growth in the absence of density-dependence; Ellner et al. 2016) and $C_j(t)$ as the ratio between maximum potential growth and realised growth (Freckleton et al. 2009, Ellner et al. 2016). Then, $r_j(t)$ can be written as:

$$r_j(t) = ln\left(\frac{E_j(t)}{C_j(t)}\right).$$

(Equation 4.10)

To test for coexistence between tabular and digitate morphologies, one of the competitors (the "resident") was simulated to be alone in the system for enough time (2000 years) to reach a stationary distribution. The other competitor (the "invader") was then introduced to the system at very low density, and the simulation was run for 1000 more years. The species in low density can successfully invade if $r_i(t) > 0$. Both competitors must be able to recover from low density when the other competitor is a resident for coexistence to be possible (Turelli 1978).

To quantify the contribution of relative nonlinearity ($-\Delta N$) and the storage effect (ΔI) to the invader's population growth rate, I used Chesson's (1994) approximations. Following Chesson (1994), I standardised $E_j(t)$ and $C_j(t)$ to units of population growth rate, and then r_j was approximated by:

$$r_j \approx \mathcal{E}_j - \mathcal{C}_j + \gamma_j \mathcal{E}_j \mathcal{C}_j.$$

(Equation 4.11)

γ_j measured the magnitude and direction of non-additivity in the model. The storage effect depends on subadditive dynamics ($\gamma_j < 0$), and a covariance between the environmental and competitive variables (χ_j; Eq. C3.11). The subscript *i* indicates that the value was associated with the invader and the subscript *r* indicates that the value was associated with the resident. The superscript -*i* indicates that species *i* was not present, and E[] denotes the expected value.

$$\chi_j^{-i} = \mathrm{E}\left[\mathcal{E}_j \mathcal{C}_j^{-i}\right].$$

(Equation 4.12)

q_{ir} is a scaling factor that weights the competition experienced by the invader according to the competition experienced by the resident. The storage effect is defined as:

$$\Delta I = \gamma_i \chi_i^{-i} - q_{ir}\gamma_r \chi_r^{-i}.$$

(Equation 4.13)

Relative nonlinearity depends on differences in the shape of the response of competition to the limiting factor (*F*). Following Kang and Chesson (2010), I chose *F* to be the resident's abundance (in terms of proportion of space covered). Competition (C_j) was then a function of the limiting factor *F*. Differences in the nonlinearity of the relationship between C_j and *F* are measured by Φ_j^2:

$$\Phi_j^2 = \left(\frac{\partial^2 C_j}{\partial F^2}\right).$$

(Equation 4.14)

The contribution of competitive nonlinearity to the invader's population growth rate depends on the differences in functional nonlinearity between the invader and the resident and in the variance in *F* when only the resident is influencing *F* ($Var(F^{-i})$ (Chesson 1994):

$$\Delta N = \frac{1}{2}(\Phi_i^2 - q_{ir}\Phi_r^2) Var\left(F^{-i}\right).$$

(Equation 4.15)

Population growth rate can be expressed in terms of the growth independent of environmental fluctuations ($\bar{r}'_i$) and the contribution of the storage effect (ΔI) and competitive nonlinearity (ΔN):

$$\bar{r}_i \approx \bar{r}'_i + \Delta I - \Delta N.$$

(Equation 4.16)

To get estimates of $\bar{r}_i$, ΔI and ΔN for each competitor, I ran 200 simulations of the competitor invading. To test if coexistence was possible in a constant environment, another set of simulations were run where the size-dependent survival was kept constant at the mean size-dependent survival in the presence of disturbance. In this way, the only difference between

both sets of simulations was the variation around mortality, not the average value of mortality (e.g. as in Descamps-Julien and Gonzalez 2005).

To confirm the accuracy of my method and code, I applied my approach to Miller et al.'s (2011) plant competition model, for which analytical estimates of the storage effect and relative nonlinearity of competition's contributions to coexistence were derived by those authors. My simulation-based estimates matched those of their study.

4.3 Results

Coexistence of tabular and digitate corals was only possible in the presence of environmental fluctuations in the form of wave action (Fig. 4.2). In a variable environment, both competitors had a positive population growth rate as invaders when the other competitor was a resident (Fig. 4.2 a & c), but in a constant environment one of the competitors was unable to invade (Fig. 4.2- b & d). The competitor that went extinct in a constant environment depended on the relative settlement probabilities of the two populations.

Relative nonlinearity of competition contributed to coexistence in my simulations, while the storage effect did not contribute to either species' population growth rate as invaders (Fig. 4.3-a & b; Fig. 4.4-a, b & c). That is, $-\Delta N$ was positive for a digitate population invading a tabular resident, and negative for a tabular population when resident. In contrast, $-\Delta N$ was approximately zero for both competitors when the tabular population was invading a digitate resident, and ΔI was approximately zero for all competitors in all cases. Visually, relative nonlinearity is apparent from the shape of the population growth rate's response to the limiting factor, which differs among competitors (Fig. 4.4-a). This difference indicates that the nonlinear average of population growth rate across a fluctuating limiting factor affected each species differently. Indeed, the digitate coral's population growth rate as

an invader would have been negative in the absence of relative nonlinearity (i.e. mean r_i is lower than $-\Delta N$; Fig. 4.3- a). In contrast, the storage effect's contribution to the invading population growth rate of both competitors is negligible ($\Delta I \approx 0$; Fig. 4.3- a & b). The absence of a storage effect can be visualized in figure 4.4-b & c, which show that the effect of competition on growth does not change depending on the environmental parameter. In other words, the effect of the environment and competition is additive on population growth rate (the slope of the response to competition does not change for high vs. low environmental parameters).

When the tabular species was a resident, it produced larger variation in the limiting factor (i.e. the proportion of space occupied by the resident; *F*) than when the digitate species was a resident (median $Var(F^{-t}) = 0.010$ (quantiles 0.05 and 0.95 being within 0.00000001 of the median); median $Var(F^{-d}) = 0.034$ (quantile 0.05=0.03 and quantile 0.95=0.043). In other words, space occupancy fluctuated more when the tabular species was the resident than when the digitate species was the resident. Additionally, each species had a higher population growth rate as an invader than as a resident (i.e. $digitate_i > digitate_r$ & $tabular_i > tabular_r$; Fig. 4.5). Furthermore, the competitor that was invading had higher population growth rate than the competitor that was a resident in both scenarios (i.e. $digitate_i > tabular_r$. & $tabular_i > digitate_r$).

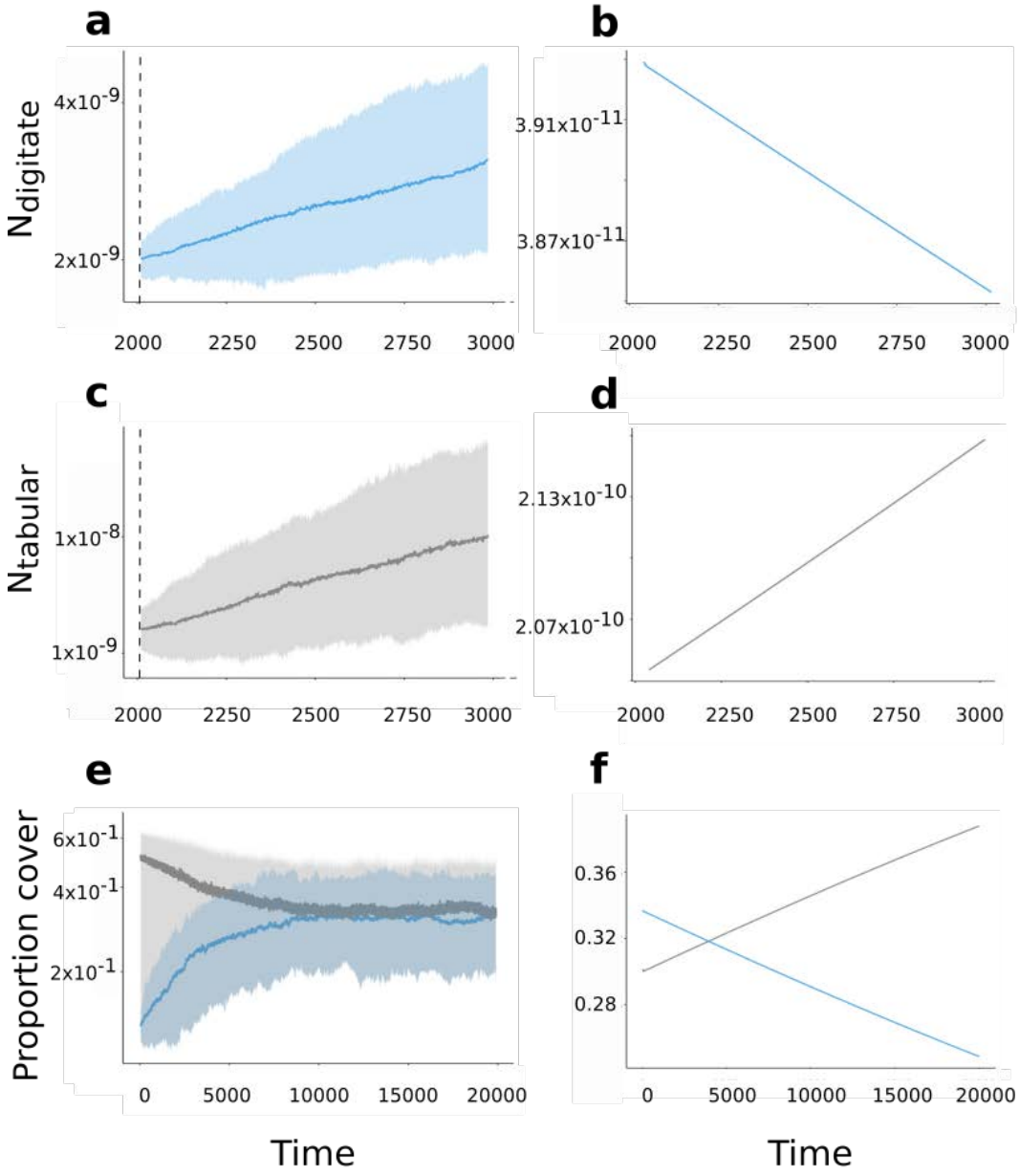

Figure 4.2. Population trajectories through time. (a) & (b) - proportion of space occupied for the digitate population (log-scale) through time (10^0 indicates 100% cover, 10^{-1} indicates 10% cover, etc.), following invasion in a variable and a constant environment, respectively. The vertical dashed line indicates the year when the digitate colonies were introduced in the system where previously tabular corals had reached their long-term abundance in the absence of competitors. (c) & (d) - proportion of space occupied for the tabular population (log-scale) through time, following invasion in a variable and a constant environment, respectively. The vertical dashed line indicates the year when the tabular colonies were introduced in the system where previously digitate corals had reached their long-term abundance in the absence of competitors. (e) & (f)- proportion of space occupied (log-scale) of tabular (in grey) and digitate (in blue) coral populations through time when both species were initially present in a variable and a constant environment, respectively. In all panels, the solid lines represent the median percent cover from the 200 simulations, and the envelopes encompass the 95% confidence interval.

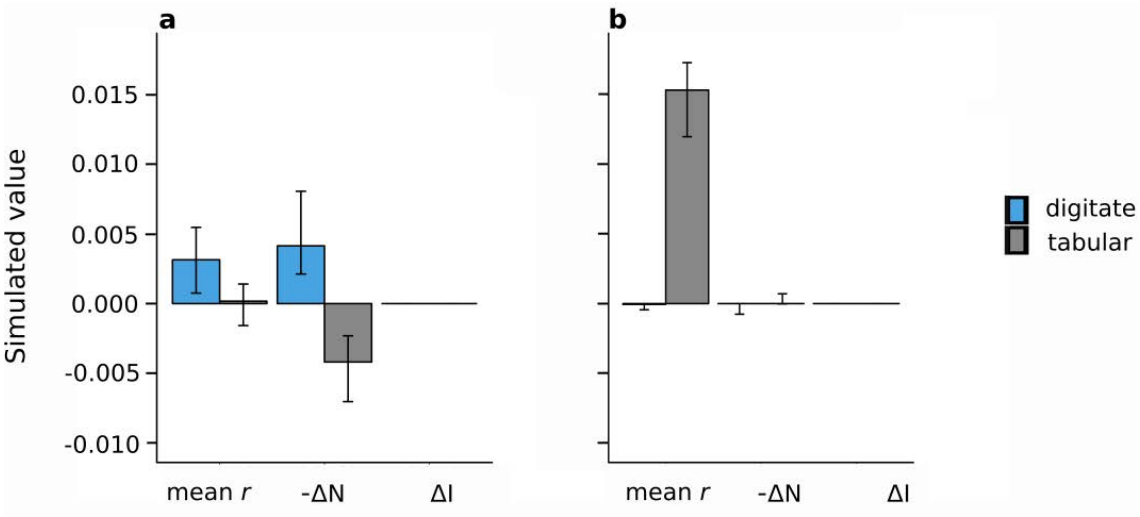

Figure 4.3. Per-capita population growth rate (mean *r*), contribution of relative nonlinearity of competition (-ΔN) to population growth rate, and contribution of the storage effect (ΔI) to population growth rate. (a) The scenario when the digitate species is an invader and the tabular species has reached its long-term abundance in the absence of the digitate competitor. (b) The scenario when the tabular species is an invader and the digitate species has reached its long-term abundance in the absence of the tabular competitor. The light blue bars represent estimates for the digitate species and the grey bars represent estimates for the tabular species. Where ΔI or -ΔN are positive, the relevant process (storage effect or relative nonlinearity) makes a positive contribution to population growth.

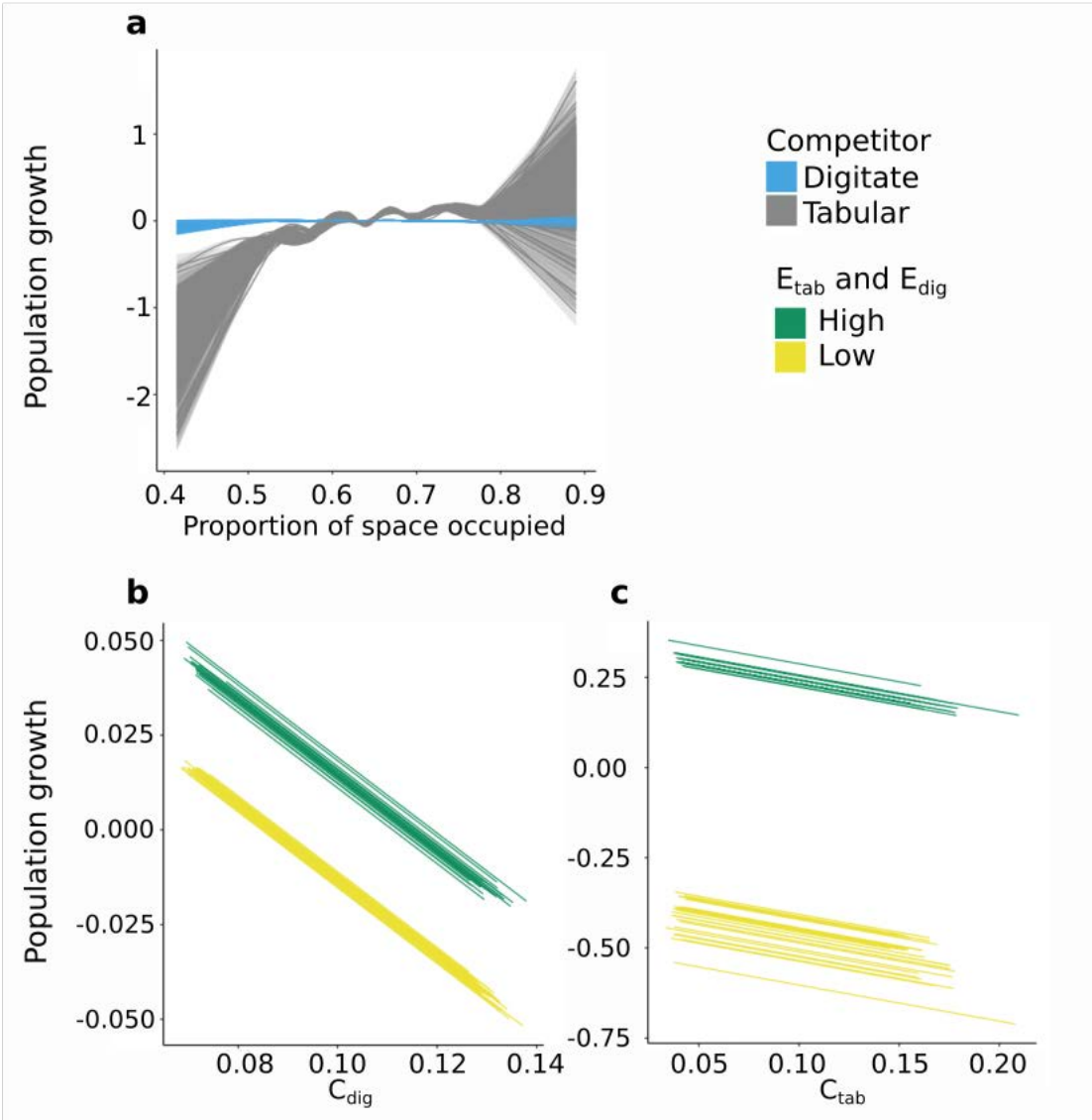

Figure 4.4. Graphical representations of relative nonlinearity and the storage effect in the presence of environmental fluctuations obtained from 200 simulations. (a) Per-capita population growth as a function of the proportion of space occupied (limiting factor) when both competitors are present. Each line shows a generalized additive model (GAM) fitted to annual per-capita population growth (expressed as the log-ratio of % cover at successive years: ln $(N(t+1)/N(t))$) as a function of the proportion of space occupied ($\sum_{i=1}^{2} N_{i,t-1}$), for one simulation (thus there is one grey line and one blue line for each simulation, representing per-capita population growth for the tabular and digitate population, respectively). (b) Growth of the digitate population as a function of C_{dig} (competition parameter for the digitate species) for the highest (green lines) and lowest (yellow lines) E_{dig} (environmental parameter for the digitate species) values, out of all E_{dig} values in each simulation. Each line represents predictions from an ordinary least-squares (OLS) regression fitted to per-capita population growth from one simulation, for years where the highest (green) or lowest (yellow) E_{dig} occurred. Panel c- Growth of the tabular population as a function of C_{tab} (competition parameter for the tabular species) for the highest and lowest E_{tab} (environmental parameter for the tabular species) values, as per panel (b). Further details on how these panels were produced is in Appendix C4 Chapter 4.

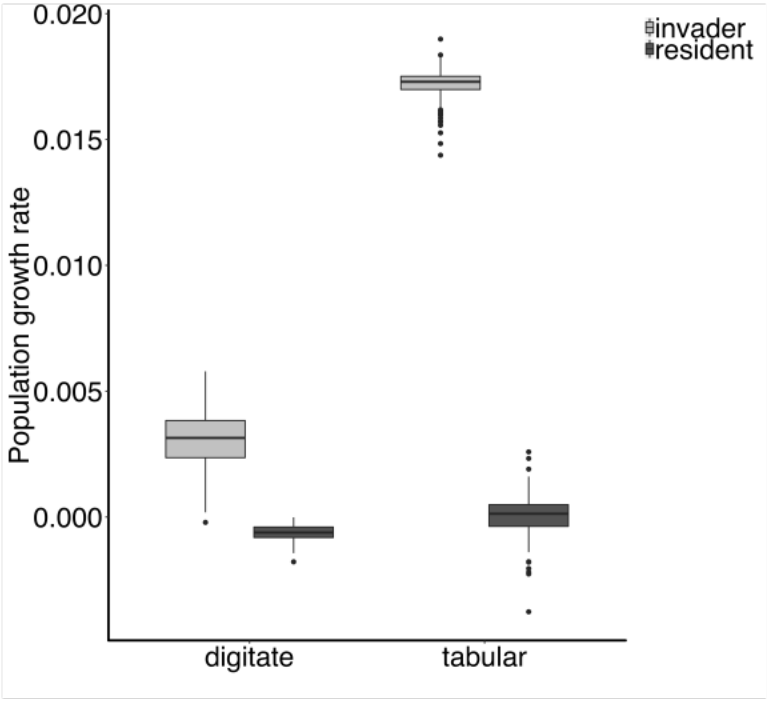

Figure 4.5. Boxplot of the per-capita population growth ($\ln\left(\frac{N(t+1)}{N(t)}\right)$) rate in 200 simulations for the digitate and tabular corals in an invader (grey) and resident (black) state.

4.4 Discussion

These findings reveal that hydrodynamic disturbances can promote the coexistence of reef-building corals via relative nonlinearity of competition, a fluctuation-dependent coexistence mechanism. In addition to temporal fluctuations in hydrodynamic forces, species must differ in their size-dependent susceptibility to hydrodynamic disturbance for this coexistence mechanism to operate. While disturbances have long being hypothesised to play a major role in the maintenance of coral biodiversity (Connell 1978, Porter et al. 1981), disturbances cannot create stabilising effects by merely reducing the intensity of species interactions (Chesson and Huntly 1997). Relative nonlinearity of competition, however, is capable of

producing stabilizing effects, because dominance of one species creates the environmental conditions that favour the recovery of its competitor.

To understand how relative nonlinearity induces a stabilizing coexistence effect, it is important to recognize that each species is favoured at different times. In periods with low hydrodynamic disturbance, tabular corals acquire new space rapidly more rapidly than digitate corals, reaching large colony sizes that are very fecund. Therefore, periods when the performance of the tabular population exceeds the performance of the digitate population are characterised by high coral cover (i.e. low availability of space for larvae to settle). When tabular corals are more abundant than digitate corals, hydrodynamic disturbances can reduce coral cover more strongly than when digitate corals are more abundant because large tabular colonies are more susceptible to dislodgment. The loss of large tabular colonies benefits the digitate population because there is more space for larvae to settle and because, since hydrodynamic disturbance does not affect large digitate colonies as strongly, there are still many highly fecund digitate colonies left to spawn. This means that the higher fluctuations in resource when tabular corals are dominant benefit the digitate population. These dynamics are consistent with empirical observations. Tabular corals grow faster than digitate corals (Dornelas et al. 2017), overtop competitors (Baird and Hughes 2000), and reach larger colony sizes that are very fecund (Álvarez-Noriega et al. 2016 [Chapter 2 of this thesis]). In periods of low hydrodynamic disturbance, tabular species can dominate the reef crest (Baird and Hughes 2000). However, hydrodynamic disturbances affect the large, very fecund, tabular colonies most strongly (Madin and Connolly 2006). Consequently, relative abundances of digitate corals tend to increase after disturbances that dislodge tabular corals (e.g. Muko et al. 2013).

In these models, unfavourable years for the abundant species did not reduce the competition experienced by the rare species and, similarly, favourable years for the abundant

species did not increase competition. Consequently, there was no covariation between environment and competition, a pre-requisite for the storage effect to operate. However, if the assumption that larvae do not compete against each other for settlement space is relaxed, covariation of the environment and competition can arise and the storage effect can promote coexistence, even in the absence of relative nonlinearity (Appendix C5). Importantly, results from Appendix C5 show that when early life-stages had strong within-cohort competition, the storage effect could promote coexistence of species of the same morphology.

Interactions between size and environment can affect population dynamics if they affect important sizes or demographic rates (Tredennick et al. 2018). The high susceptibility to hydrodynamic disturbance of the largest tabular colonies produced a trade-off between fecundity and survival which resulted in a temporal partitioning of resources via relative nonlinearity. The higher population growth rate of each species as the invader, rather than as the resident indicates that each competitor negatively affects its own population growth rate more strongly than it affects its competitor's population growth rate (i.e., in the long run, intraspecific competition exceeds interspecific competition).

This chapter identifies a mechanism by which hydrodynamic disturbance can promote coexistence, and clarifies that the episodic nature of this mortality, not simply the differential susceptibility of different corals, is an essential feature of what makes disturbance coexistence-promoting. Of course, this is not to say that other mechanisms of coexistence do not also operate in reef systems. For example, species differ in their photosynthetic response to water flow and light levels (Hoogenboom and Connolly 2009, Chan et al. 2016). Spatial heterogeneity, even at a small-scale (e.g. crevices vs. open habitats), might allow species to partition resource use. Additionally, larval dispersal can have important implications for coexistence. Stochastic larval dispersal, if not correlated among competitors, can promote coexistence (Berkley et al. 2010). Moreover, larval dispersal among patches can also promote

coexistence if there is spatial heterogeneity in demographic rates that result in each species performing better in a different patch (McPeek and Holt 1992, Muko and Iwasa 2000). Even when demographic rates of competitors remain constant across patches, dispersal can promote coexistence if the larval export to import ratio of the dominant species differs among patches (Salomon et al. 2010). However, none of these mechanisms are particularly well-suited to explaining coexistence of coral morphologies, which are closely linked to susceptibility to disturbance, and have been a key trait considered in influential studies of biodiversity maintenance on reefs (Connell 1978, Jackson 1979, Hughes 1989).

Size-dependent susceptibility to disturbance is also likely to contribute to coexistence in other systems. Size-dependent interactions of demographic rates with environmental conditions are common in many natural communities (marine fish: Genner et al. 2010; trees: Zang et al. 2012; macroinvertebrates: Kiffney and Clements 1996; etc.). However, to influence population dynamics, size-dependent interactions of demographic rates with the environment must involve demographic rates that strongly influence fitness and must impact sizes that contribute strongly to population growth (Tredennick et al. 2018). My results suggest that environmental variation can contribute to coexistence via relative nonlinearity in other systems if survival of the most productive sizes of the superior competitor are more negatively affected by environmental variation than those of the inferior competitor. In my competition model, the occasional high mortality of the largest tabular colonies changed the shapes of the relationships between the competition parameters and the limiting factor, which resulted in the tabular colonies being penalised more harshly by competition when the digitate species was invading.

Understanding how environmental variability affects community dynamics is becoming increasingly important as scientists try to understand how communities will respond to climate change (Huxman et al. 2013). Intense storms are predicted to be more frequent with

increasing sea surface temperatures (Knutson et al. 2004, Knutson et al. 2010). Additionally, ocean acidification is predicted affect calcification and result in lower skeletal density (Cooper et al. 2008), affecting colonies' susceptibility to dislodgement (Madin et al. 2008, Madin et al. 2012b). If hydrodynamic disturbance can promote coral species coexistence via fluctuation-mediated coexistence, anthropogenic changes that alter hydrodynamic disturbance regimes or species' vulnerability to mechanical disturbance will have profound effects in coral assemblages. To better anticipate such effects, improvements in our understanding of the processes maintaining biodiversity, such as that offered here, are needed.

Chapter 5: General discussion

5.1 Thesis summary

Coral assemblages are a clear example of the ‘paradox of the plankton’ (Hutchinson 1961): they can be very species-rich (Veron et al. 2011) and yet, species compete for a few limiting resources, mainly free space. Disturbance had been hypothesised to contribute to coral-species coexistence for more than three decades (Connell 1978), but the mechanisms behind such a contribution have been unknown. The overarching aim of this thesis was to investigate how coral biodiversity is maintained. The first two chapters of this thesis quantify the necessary missing demographic rates and processes to calibrate a competition model. In Chapter 2, I estimated the size-dependent fecundity relationships for a series of coral species and tested whether variation in colony fecundity is different between species of the same morphology and among morphologies. Results showed much lower variation in colony fecundity between species with a similar morphology than among morphologies, demonstrating that colony morphology can be used as a quantitative proxy for fecundity. Since it had been previously shown that mortality and growth are also much more similar between species with a similar morphology than among morphologies (Madin et al. 2014, Dornelas et al. 2017; respectively), colony morphology can be used as a functional trait in future trait-based approaches. In Chapter 3 of this thesis, I tested whether competitive displacement occurred in a natural community. Competitive displacement is required for some coexistence-promoting mechanisms, such as competition-colonization trade-offs, to operate. However, results show a negligible effect of competition on colony growth, suggesting that the assumption is not met and that competition between corals must occur at a life-stage other than adults.

In Chapter 4 of this thesis, I built process-based models of size-structured coral species interactions by extending existing integral projection models for corals and incorporating density-dependence and inter-specific competition. These models were calibrated using available demographic and environmental data (Madin et al. 2006, Madin and Connolly 2006, Madin et al. 2014, Dornelas et al. 2017) and fecundity estimates obtained in Chapter 2 of this thesis. Since the results of Chapter 3 suggested that competition between adult colonies is unlikely to strongly influence community dynamics, I only included density-dependence in larval settlement probability, with settlement being proportional to space not already occupied by adults. The analysis of the simulations from the process-based models showed that relative nonlinearity of competition can contribute to coral coexistence of species with tabular and digitate growth forms via differences in size-dependent susceptibility to disturbance. Relative nonlinearity of competition has received very little attention compared to the other fluctuation-dependent mechanism, the storage effect (e.g. Cáceres 1997, Adler et al. 2006, Angert et al. 2009). My results suggest that relative nonlinearity can be a very important coexistence-promoting mechanism in reef-building corals.

5.2 Robustness of results and future directions

Using colony morphology as the proxy for demographic rates in future trait-based approaches will at least partly help solve the problems of dimensionality that arise from investigating species-by-species interactions in species-rich assemblages. Nevertheless, demographic rates are also influenced by phylogeny and species with similar colony morphology but from distant phylogenetic branches are less likely to be similar. For example, fecundity of a

branching *Pocillopora* species and a branching *Acropora* species are unlikely to be as similar as fecundity of two branching *Acropora* species.

Although coral cover on the reef crest of Lizard Island between 2009-2013 was at the upper end of what is typical for reef crest habitats on the GBR (Osborne et al. 2011), all colonies had a (usually substantial) proportion of their periphery free of competitors. Since colonies can redirect growth to areas without competition (Romano 1990), it is possible that unless colonies are mostly surrounded by competitors, colonies will be able to maintain growth. While competition levels experienced by colonies at the site can still affect demographic rates other than growth, a previous study suggests that it should be more costly for growth than for fecundity (Tanner 1997, but see Foster et al. 2008). In reef assemblages with very high coral cover (i.e. cover much closer to 100% than at my study site), it is possible that competition among adult colonies influences community dynamics. If there is a fitness advantage for consistently winning competitive encounters when crowding is high, other coexistence-promoting mechanisms that require trade-offs involving competitive ability (e.g. competition-colonization trade-offs and intransitive competition) may be important.

The stock-recruitment relationship in coral assemblages is unknown and, because coral larvae have a dispersive stage, it is unfeasible to obtain robust estimates of the number of potential recruits produced per unit of reproduction (e.g., per egg produced). Since this parameter was unknown, I set it to values that would produce a similar level of coral cover of the resident (~50-60%) to the coral cover observed at the study site at the time the demographic estimates were obtained. For the second competitor, I investigated the parameter space that would allow for coexistence and confirmed that the second competitor would also reach a realistic coral cover (~60-70%) in the absence of the first competitor. Thus, the fact that the presence of relative nonlinearity creates a shift from competitive exclusion to coexistence in my models does not necessarily mean that this mechanism, by

itself, is sufficient to allow coexistence of these growth forms in nature. However, particularly given that tabular corals can monopolize space on reef crests in the absence of disturbance (Connell et al. 1997, Baird and Hughes 2000), it does demonstrate that relative nonlinearity makes a positive contribution to coexistence, by facilitating the persistence of populations with a more mechanically stable morphology.

Partitioning invaders' population growth rates to the contribution of different coexistence-promoting mechanisms is still a challenging task. The first theoretical attempt to partition population growth rates into contributions of the two fluctuation-dependent mechanisms used analytical approximations with Taylor series expansions (Chesson 1994). However, this method is limited to simple, unstructured models and it implicitly assumes dynamics with low fluctuations. Applying this method to new models requires very technical mathematical analyses, making a series of assumptions that may not necessarily be realistic (e.g. Angert et al. 2009). In Chapter 4, I used a method for the partitioning of the contribution of different mechanisms to coexistence that directly relates to the partitioning proposed by Chesson (1994), but which uses simulations. Chesson's (1994) method has been the basis of most studies partitioning coexistence so far (e.g. Angert et al. 2009, Miller et al. 2011, Mathias and Chesson 2013), and therefore my results can be easily compared with those studies. However, my approach fits models to the simulated data to estimate terms, which introduces error in the estimates of the mechanisms' contributions. For example, in Chapter 4 C_j was fitted as a quadratic function of the limiting factor (F), from which the second derivative was needed to quantify relative nonlinearity. Any nonlinearities beyond the quadratic term are ignored. Additionally, applying Chesson's (1994, 2003) partitioning requires a definition for environmental and competitive parameters ($E_j(t)$ and $C_j(t)$ in Chapter 4), which can be defined in terms of different quantities. For example, $E_j(t)$ was originally defined as a demographic rate that is affected by the environment but not by

competition (Chesson 1994) (e.g. the natural logarithm of the per-capita recruitment). However, in a structured model, the choice is not obvious because the environment additionally affects the size or age-distribution, so the weighted mean of all demographic rates will change. Ellner et al. (2016) suggest measuring $E_j(t)$ as the environmental variable (e.g. rainfall, wind disturbance in the model of Chapter 4), but with this approach $r_j(t)$ cannot be expressed as a function of fluctuation-independent terms, $E_j(t)$, and $C_j(t)$ only (since size-distributions and demographic rates fluctuate due to variation in $E_j(t)$), as required by the original approach to quantify the contribute of the storage effect and relative nonlinearity to coexistence (Chesson 1994). My approach for the model in Chapter 4 was to define $E_j(t)$ as the maximum potential growth, therefore incorporating all effects of a fluctuating environment in the demographic rates weighted by the size distribution. This approach allowed me to compute $r_j(t)$ as a function of $E_j(t)$ and $C_j(t)$ only, and then partition the contribution of the fluctuation-dependent mechanism as in Chesson (1994). However, ideally there should be an unambiguous definition of $E_j(t)$ and $C_j(t)$ for all models, or alternatively, coexistence ecology should be moving towards a more flexible study of coexistence.

A very recent study by Ellner and colleagues (2018) proposed a new method to quantify coexistence-promoting mechanisms using simulations or experiments, expanding the application of coexistence theory to a broader range of models with higher complexity. In this method, the difference between the invader's and the resident's population growth rates is decomposed into terms depending on particular sources of variance and their covariance, or on trait differences among species. This method provides a more flexible framework to quantify contributions to coexistence. However, it can be computationally intensive since several scenarios must be run (one for each decomposition), and it uses a different decomposition of the population growth rate than the original partitioning of coexistence

(Chesson 1994). Chesson (1994) partitions population growth rate as a sum of the population growth rate independent of fluctuations, the contribution of the storage effect, and the contribution of relative nonlinearity of competition (Chesson 1994; p. 249, Eq. 52). In contrast, Ellner et al. (2018) partition population growth rate into population growth rate in the absence of fluctuations, the contribution of the variance of individual features that fluctuate in time or space and that are important for demographic rates (e.g. fluctuations in environmental conditions, or fluctuations in the equivalent $E_j(t)$ and $C_j(t)$), and the interactions among the selected features (e.g. covariances between $E_j(t)$ and $C_j(t)$).

The models in Chapter 4 and in Appendix C5 assumed that all space available was equality suitable for both competitors. In reality, species differ in their performance across flow and light levels (e.g. Hoogenboom and Connolly 2009; Chan et al. 2016), which can differ strongly even at small scales (e.g. Anthony and Hoegh-Guldberg 2003). Differences in species' performance across environmental gradients affect their broad-scale distribution in space (Anthony and Connolly 2004), and different reef zones have different species compositions (Sheppard 1980). It is likely that differences at smaller, microhabitat scales will provide some opportunity for small-scale niche partitioning that also contributes to coral species coexistence. For such small-scale niche partitioning to promote coexistence, each species must perform better than the rest in a particular microhabitat and it must be able to disperse between microsites. In that way, if a species becomes rare, it can exploit its preferred microhabitats because, since those conditions are unfavourable for its competitors, competition should be low (Snyder and Chesson 2003).

The model in Chapter 4 is for species that co-occur on the reef crest and assumes that the community dynamics are representative of the whole-population scale. However, in reality, coral metapopulations are composed of many populations connected through larval dispersal. Connectivity among reefs has the potential to occur at very large scales (Graham et

al. 2008), while hydrodynamic disturbance tends to be more localized, depending on the orientation of the reef crest (Madin et al. 2018). Connectivity between subpopulations that differ in their environmental conditions can affect coexistence (e.g. Hanski 1999; Forbes and Chase 2002). For example, emigrants from populations in favourable environments can buffer population growth in unfavourable environments (e.g. Amarasekare and Nisbet 2001), and spatial analogues of the temporal storage effect and relative nonlinearity of competition can contribute to coexistence (Chesson 2000b). The role of spatial coexistence-promoting mechanisms in coral species coexistence is still unknown.

5.3 Broader implications and conclusions

Global warming is altering natural systems around the world (IPCC 2013). In a warmer climate, tropical cyclones are predicted to be less frequent but have a higher mean intensity (Knutson et al. 2010; Knutson et al. 2015; Sugi et al. 2017). Additionally, ocean acidification will reduce calcification rates (Kleypas et al.1999), which can cause a reduction in skeletal density (Cooper et al 2008). Lower skeletal density increases colonies' vulnerability to mechanical dislodgement (Madin et al. 2008; Madin et al. 2012b). Therefore, current rates of environmental change will modify the disturbance regimes affecting coral assemblages, as well as their response to this disturbance. Knowledge of how disturbance affects biodiversity will be important when predicting and assessing the effects of environmental change in ecological communities (Miller et al. 2011). The results of this thesis increase our understanding of how disturbance affects coral biodiversity maintenance and may be useful for predicting how coral assemblages will respond to future environmental conditions. For example, relative nonlinearity can only promote coexistence if it increases population growth of the inferior competitor enough for it to invade, but it does not decrease

population growth of the superior competitor enough to favour its extinction. The predicted increase in frequency of very strong tropical cyclones (Knutson et al. 2010) may further disadvantage tabular corals through relative nonlinearity, with potential implications for extinction risk.

In addition to storms, coral bleaching and predator outbreaks are disturbances that strongly influence coral assemblages (De'ath et al. 2012). For these disturbances to contribute to coexistence via relative nonlinearity of competition, they should impact more strongly those species that have higher population growth rates in the absence of disturbance. Coral taxonomy and morphology influence colonies' susceptibility to bleaching (Marshall and Baird 2000; Loya et al. 2001; Hoogenboom et al. 2017). However, while some studies report lower susceptibility to bleaching in slow-growing taxa that are weak competitors (e.g. massive *Porites*; Darling et al. 2012) than in fast-growing, competitive taxa (e.g. branching *Acropora;* Darling et al. 2012) (Marshall and Baird 2000; Loya et al. 2011;), others show the opposite (e.g. digitate *Acropora* colonies bleached more than tabular *Acropora* colonies in the 2016 bleaching event on Lizard Island, GBR; Hoogenboom et al. 2017). Crown of thorns starfish (*Acanthaster planci*) preys on coral colonies and is a major source of mortality when found in high densities. *Acanthaster planci* preferred prey in the central and western Indo Pacific are tabular *Acropora* (Pratchett 2007), which suggests that predator disturbance might also contribute to coexistence. However, in other regions, *A. planci* prefers rare, less competitive species, reducing coral diversity (Glynn 1976). Therefore, it is unclear how relative nonlinearity of competition can influence coexistence via these other types of disturbances.

Understanding biodiversity maintenance in species-rich assemblages remains a challenging task for ecologists. In coral assemblages, very few coexistence-promoting mechanisms have been tested and most cannot contribute to coral species coexistence, coral

coexistence remaining largely unexplained. This thesis proposes that coexistence-promoting mechanisms that require competitive displacement (e.g. competition-colonization trade-offs) are unlikely to contribute to coral species coexistence. Additionally, this thesis builds on a core ecological hypothesis: the intermediate disturbance hypothesis (Connell 1978) and shows that hydrodynamic disturbance can promote coexistence between species of different morphologies, that have different susceptibilities to dislodgement. Importantly, this thesis identifies that relative nonlinearity of competition, despite generally being thought to be a weak mechanism, was the mechanism responsible for coexistence.

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Appendix A Chapter 2

Table A.1. Parameter estimates for the probability of a polyp being fecund (logit-link), with upper and lower 95% credible intervals.

	Maturity probability					
	intercept			slope		
	lci	median	uci	lci	median	uci
A. hyacinthus	4.022	5.908	8.345	0.889	1.602	2.477
A. cytherea	0.446	1.023	1.657	0.107	0.462	0.841
A. cf. digitifera	7.309	11.507	17.142	1.252	2.277	3.572
A. humilis	9.477	14.999	22.269	1.649	2.833	4.339
A. nasuta	7.782	14.074	22.922	1.296	2.791	4.753
A. spathulata	5.933	9.496	14.107	0.973	1.838	2.916
G. pectinata	0.802	7.036	14.169	-0.594	0.771	2.126
G. retiformis	2.796	4.966	7.423	0.376	0.883	1.450
tabular	1.271	1.813	2.398	0.125	0.410	0.702
digitate	8.747	12.093	16.196	1.536	2.291	3.180
corymbose	7.575	10.724	14.673	1.323	2.081	2.993
massive	2.249	4.168	6.215	0.085	0.516	0.957

Table A.2. Parameter estimates for the number of oocytes per fecund polyp, with upper and lower 95% credible intervals.

	Oocytes per mature polyp					
	intercept			slope		
	lci	median	uci	lci	median	uci
A. hyacinthus	5.384	5.562	5.751	0.001	0.104	0.203
A. cytherea	5.009	5.146	5.291	0.088	0.021	0.129
A. cf. digitifera	7.707	8.125	8.539	0.401	0.533	0.660
A. humilis	9.309	9.924	10.543	0.620	0.777	0.934
A. nasuta	10.919	11.418	11.925	0.779	0.923	1.071
A. spathulata	5.807	6.140	6.475	0.204	0.305	0.405
G. pectinata	88.764	124.000	160.337	3.991	4.041	11.773
G. retiformis	38.975	52.098	64.873	2.280	1.207	4.271
tabular	5.197	5.306	5.416	0.058	0.009	0.076
digitate	7.501	7.822	8.151	0.244	0.334	0.423
corymbose	7.822	8.117	8.413	0.329	0.417	0.503
massive	75.204	78.251	81.514			

Table A.3. Median polyp density (polyps/cm^2), with upper and lower 95% credible intervals.

	Polyp density (polyps/cm^2)		
	lci	median	uci
A. hyacinthus	60.357	80.620	121.047
A. cytherea	49.658	74.819	129.546
A. cf. digitifera	42.757	84.030	138.829
A. humilis	50.810	59.890	72.476
A. nasuta	46.598	86.250	139.870
A. spathulata	91.178	132.306	184.118
G. pectinata	2.237	5.729	13.588
G. retiformis	8.006	11.148	18.646
tabular	65.095	75.512	89.956
digitate	51.095	62.922	78.190
corymbose	70.692	99.782	140.254
massive	5.608	7.925	12.027

Table A.4. Median carbon content (μg) per oocyte, with upper and lower 95% credible intervals.

	Egg carbon content		
	lci	median	uci
A. hyacinthus	37.633	41.286	45.466
A. cytherea	40.928	42.514	44.153
A. cf. digitifera	32.566	34.473	36.515
A. humilis	40.446	42.291	44.351
A. nasuta	24.024	27.701	31.927
A. spathulata	37.317	38.975	40.691
G. pectinata	11.331	12.958	14.802
G. retiformis	13.302	15.728	18.673
tabular	40.017	41.868	43.915
digitate	36.257	38.169	40.235
corymbose	29.680	32.768	36.113
massive	12.799	14.197	15.777

Table A.5. Median proportion of the colony outside the sterile zone, with upper and lower 95% credible intervals.

Proportion of the colony outside the sterile zone

	lci	median	uci
A. hyacinthus	0.760	0.771	0.781
A. cytherea	0.999	1.000	1.000
A. cf. digitifera	0.773	0.868	0.936
A. humilis	0.995	1.000	1.000
A. nasuta	0.970	0.999	1.000
A. spathulata	0.885	0.913	0.941
tabular	0.999	1.000	1.000
digitate	0.979	0.997	1.000
corymbose	0.994	0.999	1.000

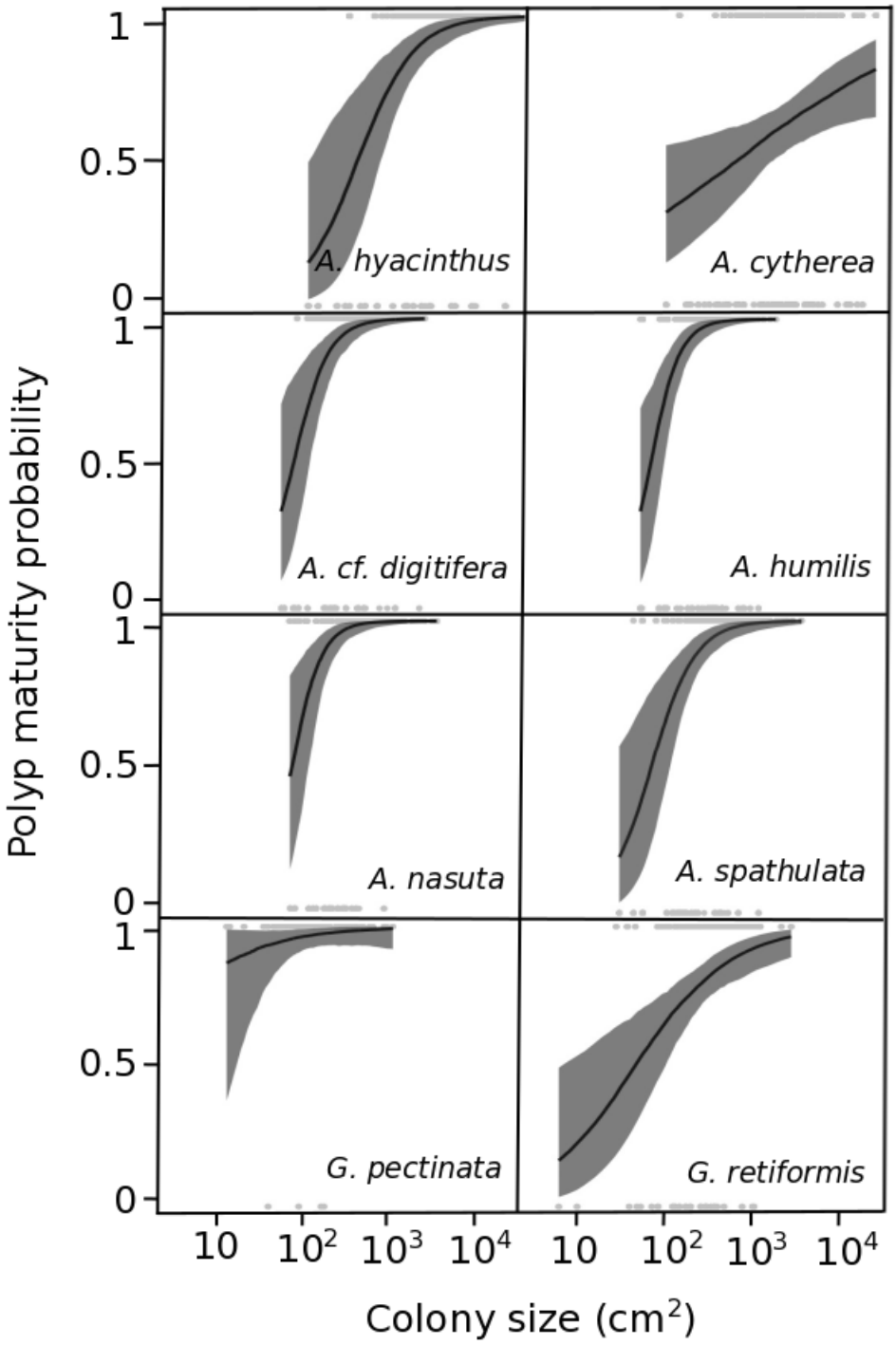

Figure A.1. Probability of a polyp being mature vs. colony size (log scale) for each species. The solid line is the regression, the grey ribbon corresponds to the 95% credible interval and the light grey circles are the observations

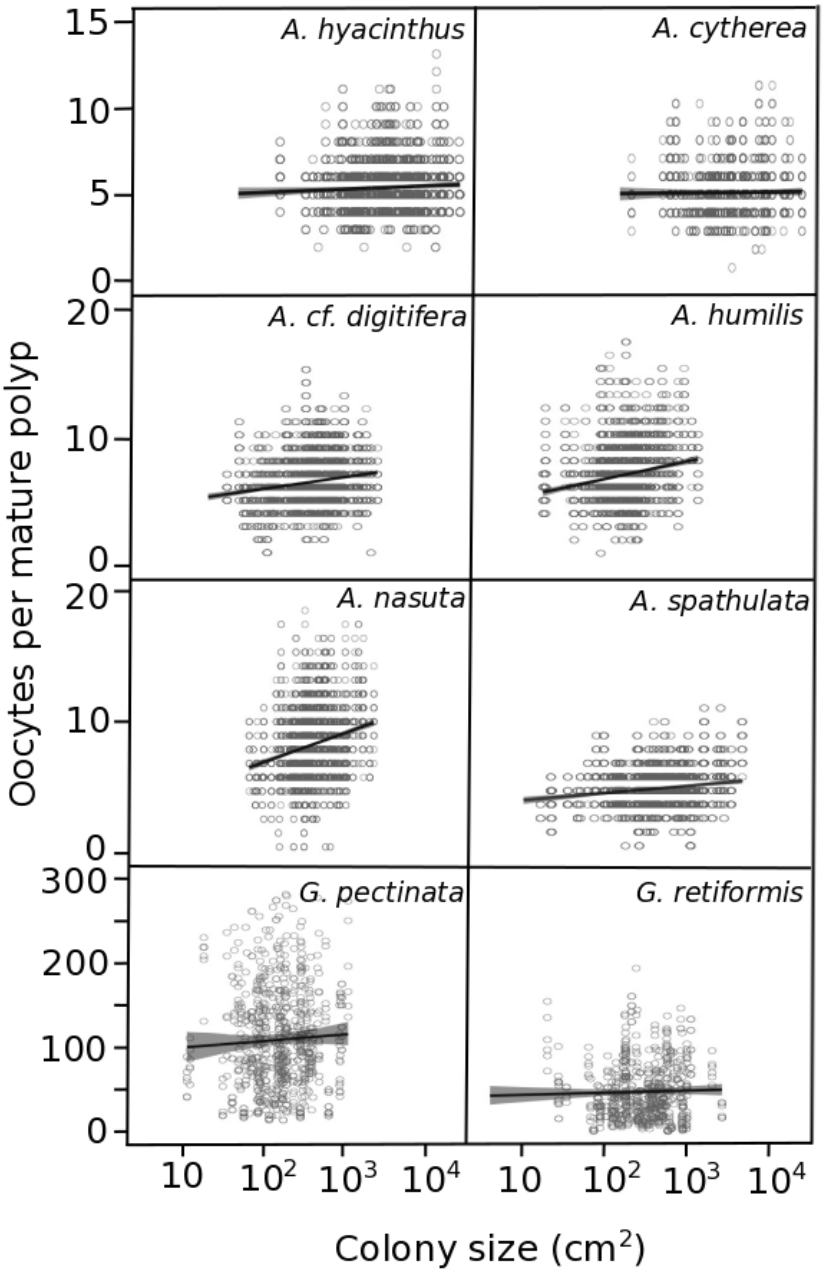

Figure A.2. Number of oocytes per mature polyp vs. colony size (log scale). The solid line is the regression, the grey ribbon corresponds to the 95% credible interval and the light grey circles are the observations. Note that the scale on the y-axis is different for massive colonies.

Appendix B Chapter 3

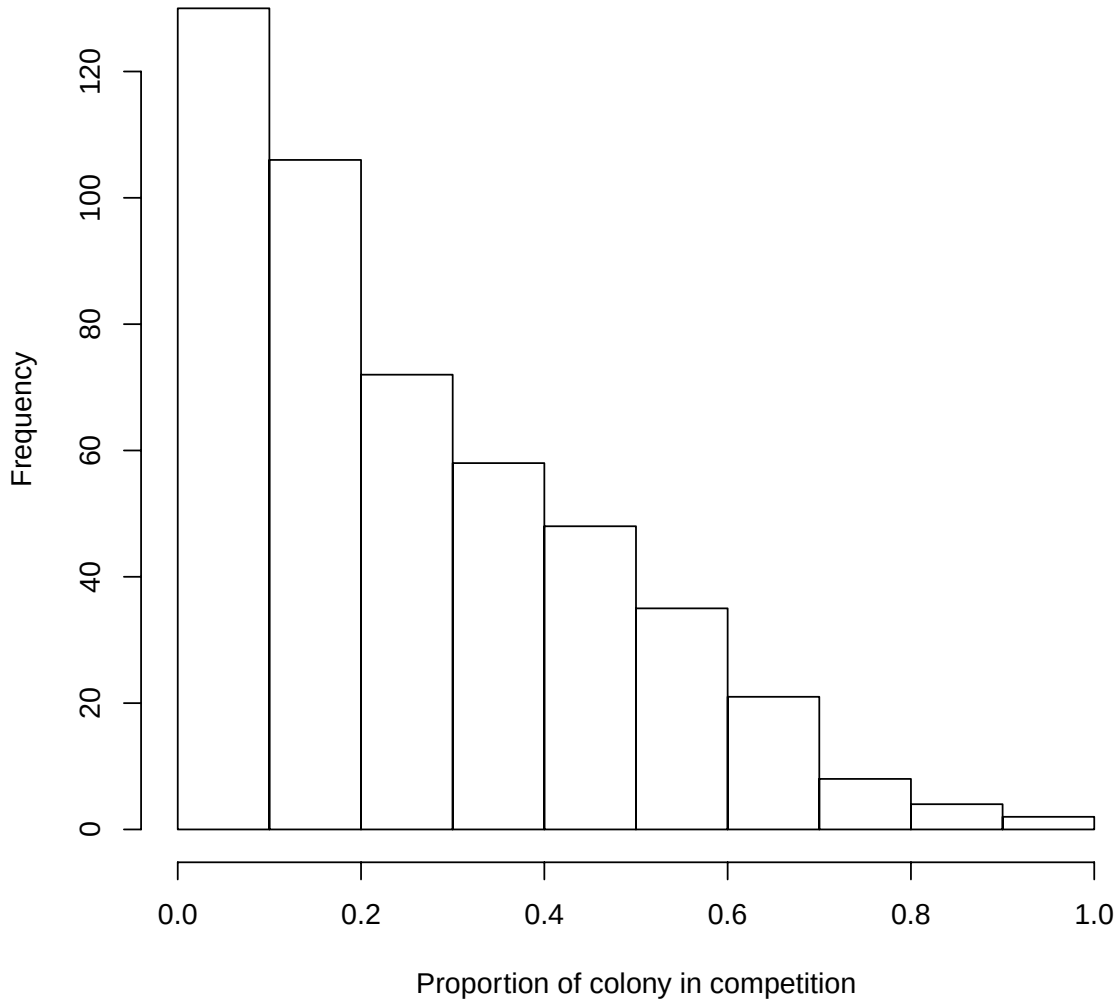

Figure B.1 Frequency distribution of the observed proportion of the colony's periphery in competition.

Table B.1. Akaike weights comparing possible models predicting colony growth with quantile regression through the 5th, 50th and 95th quantiles. Bold letters indicate the best-fit model (i.e. model with the Akaike weight closes to 1).

model	quantile=0.05	quantile=0.50	quantile=0.95
area+competition*species	-	0.1335	-
area+competition+species	-	0.0042	-
area+species	-	0.0033	-
area+competition	**0.5769**	**0.5049**	**0.5964**
competition+species	-	<0.001	-
area	0.0358	0.3541	0.4036
competition	0.3874	<0.001	0.0000
species	-	<0.001	-

Table B.2. Statistical results of the generalised linear model with binomial error structure to predict the probability of a competitor having a specific morphology given that the focal colony had that same morphology or a different one.

Branching

	Estimate	Std. Error	z value	Pr(>|z|)
(intercept)	-2.126	0.181	-11.718	**<0.0001**
Non-conspecific	-0.278	0.205	-1.353	0.176

Corymbose

	Estimate	Std. Error	z value	Pr(>|z|)
(intercept)	-1.370	0.115	-11.928	**<0.0001**
Non-conspecific	-0.010	0.134	-0.075	0.940

Digitate

	Estimate	Std. Error	z value	Pr(>|z|)
(intercept)	-2.364	0.201	-11.742	**<0.0001**
Non-conspecific	0.368	0.217	1.695	0.090

Massive

	Estimate	Std. Error	z value	Pr(>|z|)
(intercept)	-2.197	0.351	-6.254	**<0.0001**
Non-conspecific	0.144	0.360	0.400	0.689

Tabular

	Estimate	Std. Error	z value	Pr(>|z|)
(intercept)	-1.415	0.073	-19.371	**<0.0001**
Non-conspecific	0.280	0.123	2.268	**0.023**

Appendix C1 Chapter 4

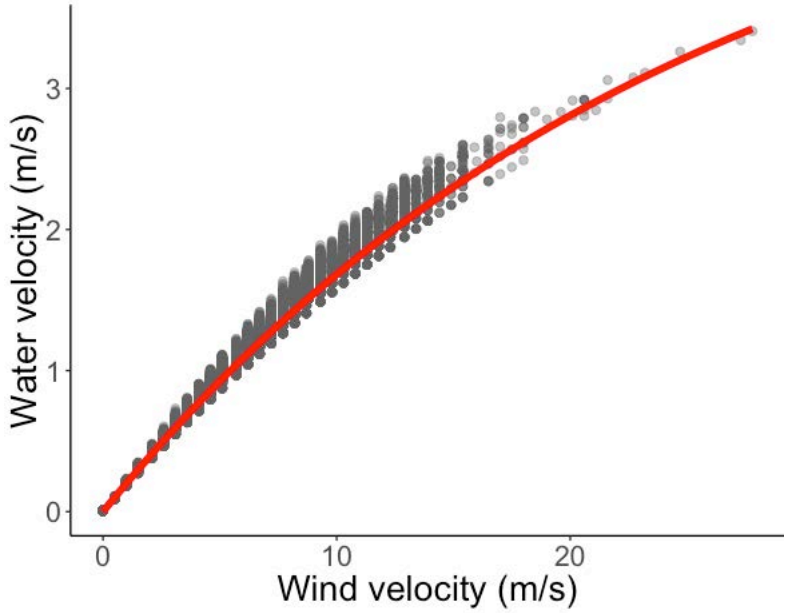

Figure C1.1. Fit model predicting water velocity (u; ms^{-1}) as a saturated function of wind velocity (v; ms^{-1}) ($u = 5.10(1 - e^{-0.04v})$). The red line shows model predictions and the grey points show the data.

Appendix C2 Chapter 4

Table C2.1. Comparisons of binomial linear models predicting disturbance-independent survival of tabular and digitate colonies with and without colony area (log-scale, cm^2) as explanatory variables.

Competitor	Model	AIC	AIC weights
tabular	log-area	41.72	0.32
	-	40.19	0.68
digitate	log-area	136.61	0.81
	-	139.51	0.19

Table C2.2. Coefficient estimates for the best-fit binomial linear models predicting disturbance-independent survival of tabular and digitate colonies.

Competitor	Effect	Estimate	Std. Error	z value	Pr(>|z|)
tabular	(intercept)	0.693	0.387	1.790	0.074
	log-area	-	-	-	-
digitate	(intercept)	-0.409	1.231	-0.332	0.740
	log-area	0.525	0.235	2.234	0.026

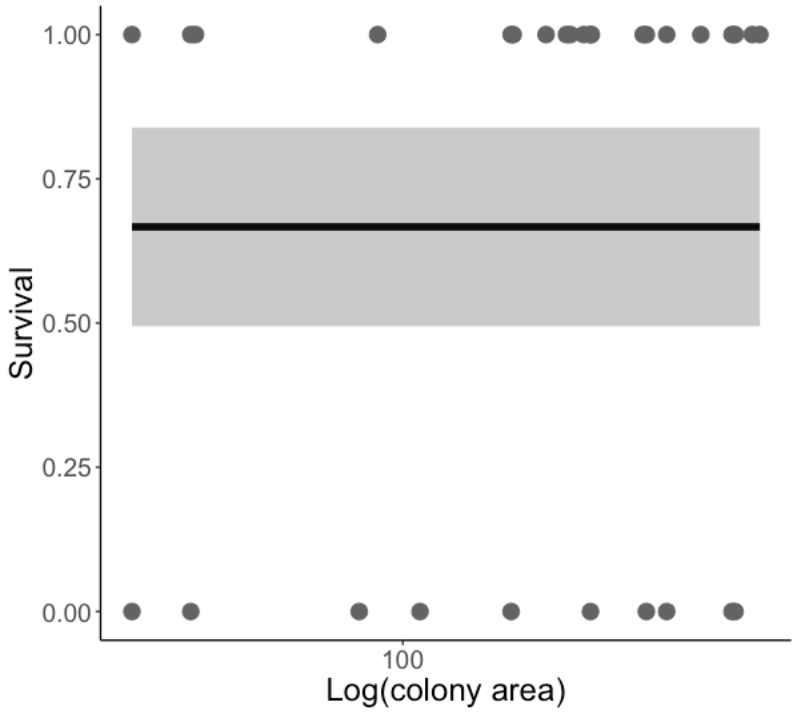

Figure C2.1. Predictions of the best-fit model predicting disturbance-independent survival of tabular colonies vs. colony size (log-scale, cm^2). The solid line shows model predictions, the grey ribbon shows standard errors, and the solid circles show the data points.

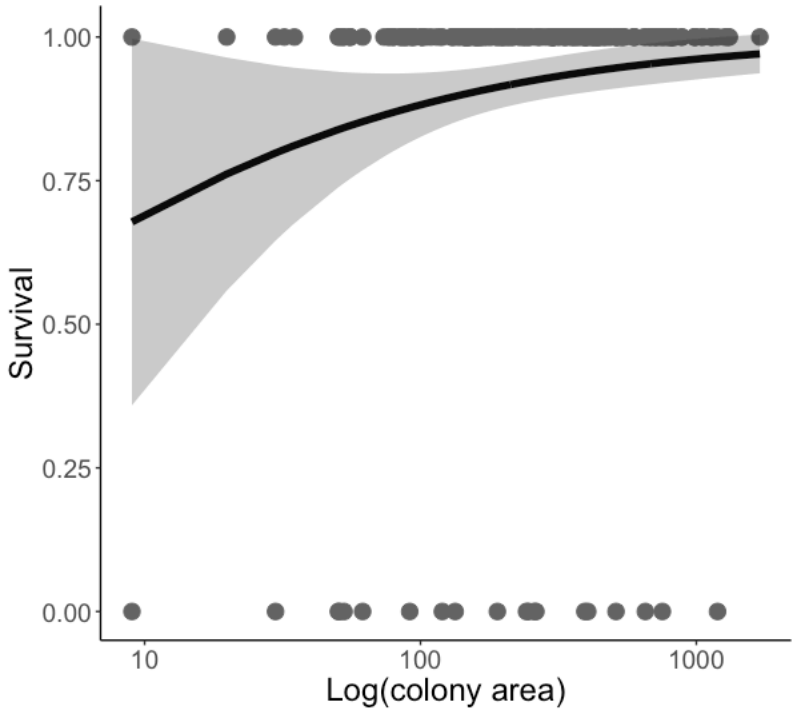

Figure C2.2. Predictions of the best-fit model predicting disturbance-independent survival of digitate colonies vs. colony size (log-scale, cm^2). The solid line shows model predictions, the grey ribbon shows standard errors, and the solid circles show the data points.

Appendix C3 Chapter 4

Detailed analysis of coexistence

Partitioning the contribution of the fluctuation-dependent mechanisms analytically is unfeasible in complex models (e.g. multiple-step, stage/size-dependent models). Simulation-based approaches to quantify mechanisms have been recently developed as an alternative when models are too complex for analytical solutions (Ellner et al. 2016; Letten et al. 2018). I use a similar approach, and estimate terms needed for the analytical solution via simulations.

Overall, the finite rate of increase of species *j* between time *t-1* and time *t* ($\lambda_j(t)$) in terms of proportion of occupied space (i.e. the factor by which the proportion of space occupied by species *j* changes) is:

$$\lambda_j(t) = \frac{N_{j,t}}{N_{j,t-1}}$$

(Equation C3.1)

and the overall population growth rate ($r_j(t)$) is:

$$r_j(t) = \ln\,[\lambda_j(t)].$$

(Equation C3.2)

If $r_j(t) > 0$, the proportion of space occupied by species *j* is increasing from time *t-1* to time *t*. The proportion of space occupied by species *j* remains the same when $r_j(t) = 0$ and decreases if $r_j(t) < 0$.

Following Chesson (1994), $r_j(t)$ can be expressed as some function g_j which depends on an environmentally dependent parameter ($E_j(t)$) and a competition parameter ($C_j(t)$):

$$r_j(t) = g_j(E_j(t), C_j(t)).$$

(Equation C3.3)

In my model, density-dependence occurs during settlement, which is limited by the proportion of free space at time t $(1 - \sum_{k=1}^{n} N_{k,t-1})$. I defined $E_j(t)$ as the maximum population potential growth ($\varphi_j(t)$; Eqs. 11 & 12) (i.e. growth in the absence of density-dependence; Ellner et al. 2016) and $C_j(t)$ as the ratio between maximum potential growth ($\varphi_j(t)$) and realised growth ($\zeta_j(t)$; Eqs. 13 & 14) (Freckleton et al. 2009; Ellner et al. 2016).

$$\varphi_j(t) = \frac{\int_0^\infty y\{\int_0^\infty S_{j,t-h}(x')G_j(x',y)[n_j(x,t-1) + \int_0^\infty F_j(x,x')n_j(x,t-1)dx]dx'\}dy}{N_{j,t-1}}$$

(Equation C3.4)

$$E_j(t) = \varphi_j(t)$$

(Equation C3.5)

$$\zeta_j(t)$$

$$= \frac{\int_0^\infty y\{\int_0^\infty S_{j,t-h}(x')G_j(x',y)[n_j(x,t-1) + (1 - \sum_{k=1}^{n} N_{k,t-1}) \int_0^\infty F_j(x,x')n_j(x,t-1)dx]dx'\}dy}{N_{j,t-1}}$$

(Equation C3.6)

$$C_j(t) = \frac{\varphi_j(t)}{\zeta_j(t)}$$

(Equation C3.7)

Given these definitions for $E_j(t)$ and $C_j(t)$, $r_j(t)$ can be expressed as:

$$r_j(t) = ln\left(\frac{E_j(t)}{C_j(t)}\right).$$

(Equation C3.8)

$C_j(t)$ fluctuates because it depends on the amount of free space, and therefore there is a potential for the storage effect to operate.

To test for coexistence between tabular and digitate morphologies, one of the competitors was simulated to be alone in the system for enough time (2000 years) to reach a stationary distribution (this competitor is called the resident). The other competitor (i.e. the invader) was then introduced to the system at density lower than 1×10^{-8} proportion of space occupied, and the simulation was run for 1000 more years. The species in low density can successfully invade if $r_i(t) > 0$. Both competitors must be able to recover from low density when the other competitor is a resident for coexistence to occur (Turelli 1978).

The environmental (E_j) and competitive (C_j) parameters are non-unique and differ in meaning and in units among different models. For example, in the lottery model, E_j is in units of number of juveniles (log-scale) (Chesson 1994), whereas in my model E_j is in units of proportion of space occupied. To standardise these parameters to units of population growth rate, Chesson (1994) introduced two new parameters ($\mathcal{E}_j$ and $\mathcal{C}_j$ instead of E_j and C_j). $\mathcal{E}_j$ and $\mathcal{C}_j$ are defined relative to some baseline environment (E_j^*) and competition (C_j^*). E_j^* and C_j^* must satisfy the following condition (Chesson 1994):

$$g_j\left(E_j^*, C_j^*\right) = 0.$$

(Equation C3.9)

E_j^* is a central value (mean or median) of E_j, which then fixes the value for C_j^*. I defined $E_j^* = median(E_j)$, and then for r_j to be 0, $C_j^* = E_j^*$. The standardised parameter C_j^* is then the level of competition that reduces growth to zero in the baseline environment. Then, $\mathcal{E}_j = g_j\left(E_j, C_j^*\right)$ and $\mathcal{C}_j = -g_j\left(E_j^*, C_j\right)$ (Chesson 1994 p. 236), which gives $\mathcal{E}_j = ln\left(\frac{E_j(t)}{C_j^*(t)}\right)$, and $\mathcal{C}_j = -ln\left(\frac{E_j^*(t)}{C_j(t)}\right)$. If $\mathcal{E}_j(t) > 0$, the environment at time *t* is more favourable than the baseline

environment. If $\mathcal{C}_j(t) < 0$, competition at time *t* is low enough to allow for population growth under baseline environmental conditions. Following Chesson (1994), the population growth rate can be approximated by (Chesson 1994):

$$r_j \approx \mathcal{E}_j - \mathcal{C}_j + \gamma_j \mathcal{E}_j \mathcal{C}_j$$

(Equation C3.10)

γ_j measures the level of additivity in the model. If γ_j is negative, the interaction between $\mathcal{E}_j$ and $\mathcal{C}_j$ is subadditive, which means that the reduction in r_j caused by $\mathcal{C}_j$ is smaller in years when the environment is unfavourable than when it is favourable (Chesson 1994). This means that the species does not experience times with unfavourable environmental conditions and high competition, which reduces its risk of going extinct. Additive ($\gamma_j = 0$) and superadditive ($\gamma_j > 0$) interactions do not favour coexistence via the storage effect. γ_j was estimated by minimising sum of squares when using the values of $\mathcal{E}_j, \mathcal{C}_j$ and r_j obtained from the simulations.

In addition to subadditivity, the storage effect depends on the covariance between the environmental and competitive variables (χ_j^{-i}; Chesson 1994):

$$\chi_j^{-i} = \mathrm{E}\left[\mathcal{E}_j \mathcal{C}_j^{-i}\right].$$

(Equation C3.11)

I will use the subscript *i* for values associated with the invader and *r* for values associated with the resident. The superscript *-i* indicates that species *i* is not present (i.e. it is the invader), and E[] denotes the expected value. Since competition experienced by the invader and the resident is not necessarily equal, a new parameter (q_{ir}) is introduced to weight the invader according to its comparison to the resident (Chesson 1994).

$$q_{ir} = \left(\frac{1}{n-1}\right)\frac{\beta_i}{\beta_r}$$

(Equation C3.12)

$\beta_j = \frac{\partial c_j}{\partial c_j}$ and n is the number of species (Chesson 1994). I estimated β_j as the slope of a linear regression of c_j as a function of C_j (Ellner et al. 2016). The contribution of the storage effect to the population growth rate of the invader in two-species competition is then defined by (Chesson 1994):

$$\Delta I = \gamma_i \chi_i^{-i} - q_{ir} \gamma_r \chi_r^{-i}.$$

(Equation C3.13)

Relative nonlinearity depends on differences in the shape of the response of competition to the limiting factor (*F*). The limiting factor *F* must affect the level of competition experienced by the species. Following Kang and Chesson (2010) I chose *F* to be the resident's abundance (in terms of proportion of space covered), which is negatively proportional to the total amount of free space. Competition (C_j) is then a function of the limiting factor *F*. To allow for nonlinearities in the relationship between C_j and *F*, I fitted C_j as a quadratic function of *F* (Chesson 1994, p. 247) by minimising sum of squares. Differences in the nonlinearity of the relationship are measured by Φ_j^2, which is the second derivative of C_j with respect to *F* (Chesson 1994):

$$\Phi_j^2 = \left(\frac{\partial^2 C_j}{\partial F^2}\right).$$

(Equation C3.14).

The contribution of competitive nonlinearity to the invader's population growth rate depends on the differences in functional nonlinearity between the invader and the resident and in the variance in *F* when only the resident is influencing *F* ($Var(F^{-i})$). The resident's nonlinearity is weighted by the competition experienced by the resident relative to the invader, q_{ir} (Chesson 1994).

$$\Delta N = \frac{1}{2}(\Phi_i^2 - q_{ir}\Phi_r^2) Var\left(F^{-i}\right)$$

(Equation C3.15)

Population growth rate can be expressed in terms of the growth independent of environmental fluctuations (or dependent on fluctuations that occur within a year) ($\bar{r}'_i$) and the contribution of fluctuation-dependent coexistence mechanisms: the storage effect (ΔI) and competitive nonlinearity (ΔN) (Chesson 1994):

$$\bar{r}_i \approx \bar{r}'_i + \Delta I - \Delta N.$$

(Equation C3.16)

Since only negative values of ΔN contribute positively to the invader's population growth rate, r_i is favoured by competitive nonlinearity when $\Phi_i^2 < q_{ir}\Phi_r^2$.

To get estimates of $\bar{r}_i$, ΔI and ΔN for each competitor, I ran 200 simulations of the competitor invading. $\bar{r}_i$ was estimated as the mean population growth rate from 10 years after the invasion (to reduce behaviour influenced by the initial invading conditions) to the end of the simulations, when the invader was still rare. ΔI and ΔN were also estimated from data simulated from 10 years after the invasion to the end of the simulations.

To test if coexistence was possible in a constant environment, another set of simulations were run where the size-dependent survival was kept constant for the tabular species and no mechanical disturbance was included. The size-dependent survival of the tabular species was fixed at the mean survival in the presence of environmental fluctuations. I systematically varied the (unknown) settlement probability parameter of the digitate species, to determine if there was a region of parameter space for which coexistence was possible in the absence of fluctuations.

Appendix C4 Chapter 4

200 simulations with both competitors present were run for 3000 years. In each year of each simulation, the competitive (C_{dig} and C_{tab}) and environmental (E_{dig} and E_{tab}) parameters were calculated, as well as each competitors' population growth and the proportion of space occupied (i.e., the limiting factor). To quantify nonlinearities in the relationship, I fitted a generalized additive model (GAM) to characterize per-capita population growth as a function of the proportion of space occupied. To do this, I used the function *gam( )*of the package 'mgcv' (Wood 2011). If relative nonlinearity of competition is present, one would expect that the species with the per-capita population growth advantage would change as a function of the limiting factor (see Chesson 2000a, Fig. 1). To quantify nonadditivity (i.e., storage effect), I fitted a linear model predicting population growth with the environmental parameter, the competitive parameter, and an interaction between the two parameters as explanatory variables. I used the function *lm( )* in the package 'stats' (R Core Team 2018). If there is a storage effect, there should be an interaction such that the difference in per-capita population growth rates at low competition should be greater than it is at high competition (see Chesson 2000a, Fig. 2).

Appendix C5 Chapter 4

The results presented in the main text of Chapter 4 showed that relative nonlinearity of competition, a fluctuation-dependent mechanism, can contribute to coexistence between coral species that strongly differ in their responses to hydrodynamic disturbance, a susceptibility that is tightly linked to colony morphology (Madin and Connolly 2006). However, the contribution of relative nonlinearity is limited when species have similar morphologies because they respond very similarly to disturbance, suggesting that other coexistence-promoting mechanisms must be operating among species that share a similar morphology. In addition to hydrodynamic disturbance which affects survival, other environmental fluctuations cause high variations in recruitment across space and time (Connell et al.1997, Hughes et al.1999). The storage effect, another fluctuation-dependent mechanism, can arise from recruitment variability (aaf 1981), and it is thought to be more common and contribute to species coexistence more strongly than relative nonlinearity (Chesson 1994, Abrams and Holt 2002). The storage effect has been shown to promote coexistence in other systems (e.g. Chesson and Warner 1981, Cáceres 1997, Angert et al. 2009), and the general requirements for the mechanism to operate are well known (Chesson 1994, Chesson 2000a).

The model presented in the main text of Chapter 4 did not allow for covariation between the environment and competition, a requirement of the storage effect. However, there are reasons to believe that corals can meet the preconditions for the storage effect to operate: covariation of the environment and competition, uncorrelated responses to the environment among species, and a life stage that is resistant to competition where the benefits of favourable years can be ‘stored’. In corals, competition among larvae should increase when common species experience favourable conditions, since there will be a large number

of larvae produced overall. In contrast, competition among larvae should decrease when the common species experiences unfavourable conditions, because there will be fewer larvae produced overall. Moreover, there is high temporal variation in coral settlement, at least some of which is likely due to environmental conditions that influence per-polyp fecundity or larval survival (Harrison and Wallace 1990, Dunstan and Johnson 1997). Species have different size-dependent responses to environmental disturbance from wave action (Massel and Done 1993, Madin and Connolly 2006) and bleaching (Marshall and Baird 2000, Loya et al. 2001). Changes in population size-structure caused by size-dependent selectivity of mortality caused by disturbance, coupled with size-dependent reproduction (Hall and Hughes 1996), produces fluctuations in fecundity per unit area of habitat occupied, and thus potentially in the density of settling larvae. Finally, corals have a long-lived adult stage that is resistant to competition (Chapter 3), and, consequently this life-stage can buffer the population against years when per-capita recruitment is low.

The purpose of this appendix is to investigate the conditions under which the storage effect can contribute to coral species coexistence by allowing the environment and competition to covary. To do this, I used a lottery-type competition model, where species compete for a 'lottery' of resources (space) and each larva is a ticket. In this type of competition, free space is generated when individuals die, and the availability of free space is unpredictable. Free space is randomly allocated to the larvae. This competition model was proposed by Sale (1977) to explain the high diversity of reef fishes.

The model included two competitors with identical growth and post-settlement survival rates which were constant through time. The annual per-capita production of successful settlers (recruitment rate) differed between competitors, while keeping the long-term mean almost identical. The recruitment rate of one of the competitors was multiplied by a randomly generated factor ($v_{j,t}$) from a lognormal distribution ($X \sim N(\mu = \log(1.01) - \frac{\sigma^2}{2}$,

$\sigma^2 = 0.2$), such that $E[e^X] = 1.01$) (i.e. the superior competitor) in each year of the simulation, while the recruitment rate of the other competitor was multiplied by a randomly generated factor ($v_{j,t}$) from a lognormal distribution ($X \sim N(\mu = \log(1.00) - \frac{\sigma^2}{2},\ \sigma^2 = 0.2)$, such that $E[e^X] = 1.00$) (i.e. the inferior competitor), independently of the superior competitor (i.e., fluctuations were uncorrelated between species). The very small difference in mean recruitment rate was introduced so that, in the absence of stabilising mechanisms (the storage effect in this case), the inferior competitor would follow a clear decline in abundance through time.

An integral projection model (IPM; Easterling et al. 2000), similar to the one built for the model presented in the main text, was used to characterise community dynamics. The growth, survival, and fecundity of both competitors were calibrated using the demographic estimates for the tabular competitor in Chapter 4. No stochastic mechanical disturbance was imposed; rather, survival of species *j* at time *t-h* (where h ∈[1-z,1) and z→0) ($S_{j,t-h}(x')$) was kept at the size-dependent mean survival in the presence of mechanical disturbance obtained in Chapter 4:

$$S_{j,t-h}(x') = 1 - M_j(x').$$

(Equation C5.1)

In contrast to $M_j(x')$ in the main text, in this model $M_j(x')$ is the size-dependent mean survival in the presence of mechanical disturbance (instead of the 'background' mortality). In contrast to the competition model in the main text, space was saturated in this model. Mortality and growth were simulated to occur first, vacating space for larvae to colonize. Reproduction and settlement were simulated to happen just before the census, saturating all space vacated by mortality. In this model, $n_j(y, t-h)$ is the population density size y of species j at time *t-h* after survival ($1 - M_j(x)$) and growth ($G_j(x, y)$), rather than after recruitment:

$$n_j(y, t-h) = \int_0^{\infty} \left(1 - M_j(x)\right) G_j(x, y) n_j(x, t-1) dx.$$

(Equation C5.2)

Space available after growth and mortality ($N_{j,t-h}$) was then calculated by:

$$N_{j,t-h} = \frac{\int y[n_j(y,t-h)]dy}{A},$$

(Equation C5.3)

where *A* is the total habitat area.

Immediately before census, larvae compete for space via lottery competition. I included a term ($v_{j,t}$) to incorporate random variation in larval production. To simulate lottery competition, I first estimated the proportion of space that larvae from each species would occupy at time *t* in the absence of competition ($R_{j,t}$):

$$R_{j,t} = \frac{\int_0^{\infty} y[v_{j,t} \int_0^{\infty} F_j(y,y)\, n_j(y,t-h)dy]dy}{T}.$$

(Equation C5.4)

Note that $R_{j,t}$ is not the same as $R_j(y, t-h)$ from the competition model in Chapter 4. Here $R_{j,t}$ is equivalent to $N_{j,t}$ (i.e. the total proportion of space occupied) but restricted to recruits only. The proportion of successful recruits for species *j* ($l_{j,t}$) depends on the relative abundance of the proportion of space that larvae from species *j* would occupy in the absence of competition (in this case *k*=2):

$$l_{j,t} = \frac{R_{j,t}}{\sum_{i=1}^{k} R_{i,t}}.$$

(Equation C5.5)

Since space is assumed to be saturated, the proportion of space occupied by species *j*'s larvae ($L_{j,t}$) will depend on species *j*'s proportion of successful recruits ($l_{j,t}$) and on the amount of space available ($1 - \sum_{i=1}^{k} N_{i,t-h}$):

$$L_{j,t} = l_{j,t}\left(1 - \sum_{i=1}^{k} N_{i,t-h}\right).$$

(Equation C5.6)

To estimate the number of larvae that fit into the proportion of space equivalent to $L_{j,t}$, $L_{j,t}$ was multiplied by the total habitat area (A) to calculate the total area occupied by species j's larvae. Then, this quantity was divided by recruit size (p):

$$u_j(p,t) = \frac{L_{j,t}A}{p}.$$

(Equation C5.7)

$u_j(y,t)$ is a vector containing zeros for all colony sizes except for when y=p. Population density of species j at time t was then:

$$n_j(y,t) = n_j(y,t-h) + u_j(y,t).$$

(Equation C5.8)

Finally, the proportion of space occupied by species j at time t was:

$$N_{j,t} = \frac{\int y[n_j(y,t)]dy}{A}.$$

(Equation C5.9)

200 simulations were run in which the inferior competitor was introduced in very low densities ($<1\text{x}10^{-8}$) while the superior competitor was at its long-term abundance in the absence of the invader to test for coexistence. To quantify the contribution of the storage effect to coexistence, $E_j(t)$ and $C_j(t)$ were defined. For the partitioning of population growth rate to be possible, $E_j(t)$ and $C_j(t)$ must have upper and lower bounds. However, this model is space-saturated rather than recruitment-limited, and therefore, defining the environmental parameter ($E_j(t)$) as per-capita (or, more precisely, per-unit-area) population growth in the

absence of density-dependence could result extremely large values, particularly as $N_{t-1} \to 0$. Consequently, I use definitions for $E_j(t)$ and $C(t)$ ($C_1(t) = C_2(t) = C(t)$) that are analogous to those proposed by Chesson (1994; Eq. 83 & 86, pp. 257-258) for an unstructured lottery-model (Eq. 5.11 & 5.12). $E_j(t)$ is the natural logarithm of the per-unit area recruitment rate, and $C(t)$ is the natural logarithm of the total amount of space to be occupied by recruits, divided by the total amount of available space.

$$E_j(t) = \ln\left(\frac{R_{j,t}}{N_j, t-1}\right)$$

Equation C5.10

$$C(t) = \ln\left(\frac{\sum_{i=1}^{k} R_{i,t}}{1 - \sum_{i=1}^{k} N_{i,t-h}}\right)$$

Equation C5.11

Population growth rate ($r_j(t)$) was then defined as:

$$r_j(t) = ln\left(\frac{N_{j,t-h}}{N_{j,t-1}} + e^{E_j(t) - C(t)}\right),$$

Equation C5.12

Since the density-independent component of $r_j(t)$, $\frac{N_{j,t-h}}{N_{j,t-1}}$, was dependent on the distribution of population sizes at time *t*-1 (in $n_j(x, t-1)$), the standardised environmental and competition parameters $\mathcal{E}_j$ and $\mathcal{C}_j$, could not be estimated (since they depend on a function $g_j\big(E_j(t), C(t)\big)$, which must be independent of size-structure). Therefore, I used a method proposed by Ellner et al. (2016) in which the covariance between the environment and competition (a requirement for the storage effect) is removed, and population growth rates with and without the covariance are compared.

Using Chesson's (1994) partitioning of population growth rate:

$$\bar{r}_i \approx \bar{r}'_i + \Delta I - \Delta N,$$

(Equation C5.13)

relative nonlinearity of competition ($-\Delta N$) was calculated depending on the mean population growth rate ($\bar{r}_i$), the mean population growth rate in the absence of environmental variability ($\bar{r}'_i$), and the contribution of the storage effect to coexistence (ΔI). Estimated this way, the quantity $-\Delta N$ can include nonlinearities dependent on the environmental parameter ($E_j(t)$), in addition to nonlinearities from the competition parameter ($C_j(t)$) (Ellner et al. 2018), but I will refer to $-\Delta N$ as relative nonlinearity for simplicity. To estimate mean population growth rate in the absence of environmental variability ($\bar{r}'_i$), the mean value of $v_{j,t}$ ($\overline{v_{j,t}}$) was computed for each run of the simulation. Then, another set of simulations was run using a constant value of $v_{j,t}$ ($v_{j,t}$=$\overline{v_{j,t}}$).

Results from the simulation show that the inferior competitor could successfully invade (Fig. 5.1) and that the storage effect made a positive contribution to the invader's per-capita population growth (Fig. 5.3). Additionally, the per-capita population growth rate of the resident was lower than the per-capita population growth of the invader.

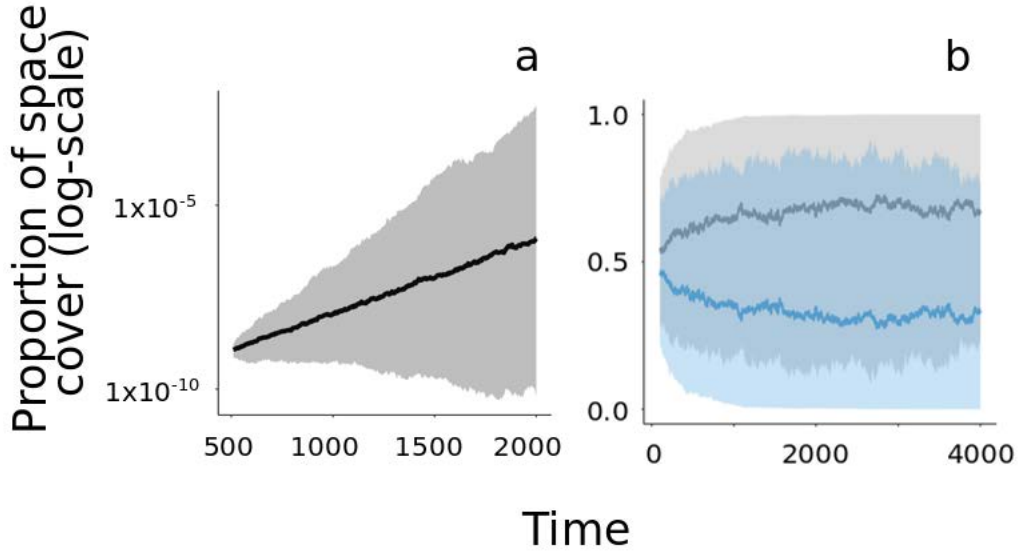

Figure C5.1. Proportion of space occupied through time. Panel a- Proportion of space occupied by the inferior competitor (log-scale) through time following invasion. The superior competitor was at its long-term abundance in the absence of the invader. Panel b- Proportion of space occupied (log-scale) of the inferior competitor (in blue) and the superior competitor (in grey) coral populations through time when both competitors were initially abundant. The solid lines represent the median proportion cover from the 200 simulations, and the envelopes encompass the 95% confidence interval.

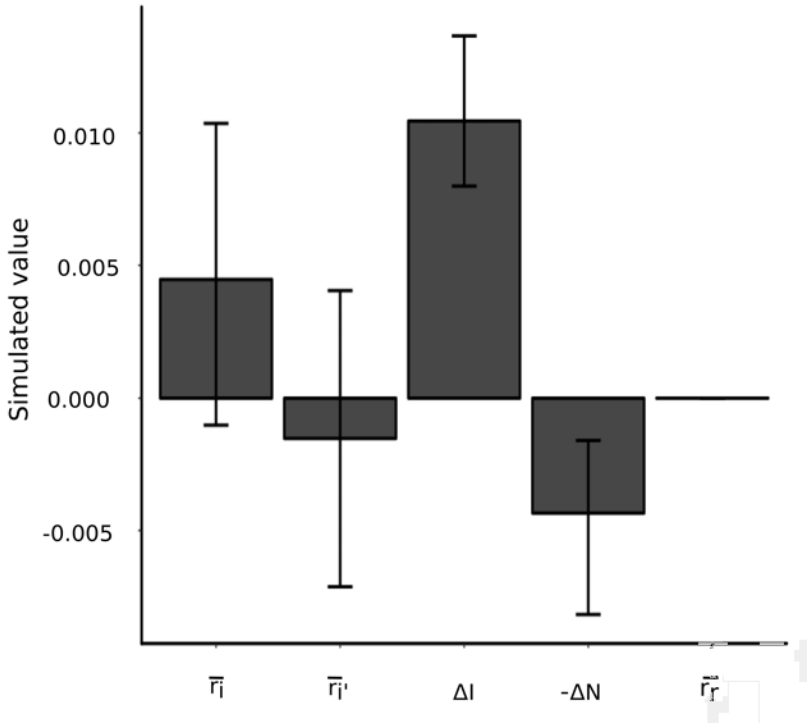

Figure C5.2. Per-capita population growth rate of the inferior competitor invading ($\bar{r}_i$), per-capita population growth rate in the absence of environmental variability ($\bar{r}'_i$), contribution of the storage effect to the invader's population growth rate (ΔI), contribution of relative nonlinearity to the invader's population growth rate (-ΔN), and per-capita population growth rate of the superior competitor when abundant ($\bar{r}_r$). The estimates were obtained for the scenario when the inferior competitor was an invader and the superior competitor had reached its long-term abundance in the absence of the inferior competitor. The bar plot represents the median estimate from 200 simulations, and the error bars encompass the 95% confidence interval.

In this model, favourable years for the abundant species resulted in more larvae competing for space unoccupied by adults and, because competition was high, the advantage gained by the abundant species in favourable years was reduced. When the rare species experienced a favourable environment, few larvae were produced overall (in comparison to years that favoured the abundant species), and therefore competition was lower. This means that, the storage effect could promote coexistence because competition and environmental fluctuations covaried in such a way that the rare species was given a disproportionate advantage in favourable years. If density-dependence in post-settlement mortality in coral assemblages is strong enough that per-settler mortality is much higher in years that favour the

abundant species compared to years that favour the rare species, the pre-conditions for a storage effect to promote coral species coexistence could be met. These results show that the storage effect can promote coexistence among species of the same morphology if early-life stages experience strong intra-cohort competition.